# Large herbivore stocking rate effects on plant palatability, forage preference and soil properties in an Alluvium Fynbos-Renosterveld mosaic

**By**

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# DECLARATION

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# ABSTRACT

An understanding of the interactions of herbivores, plant nutrients and soil properties is crucial for grazing management. Of particular interest are plant palatability and herbivore grazing preferences. These aspects, the focus of this thesis, were studied in a Swartland Shale Renosterveld and Swartland Alluvium Fynbos mosaic in the Western Cape of South Africa. This vegetation is classified as critically endangered due to the transformation of its landscape in favour of agricultural production and urban settlement.

Pre-colonial herbivore vertebrates were hunted out by 1700, leading to a sparse knowledge of the early dynamics of the vegetation. However, currently game farmers and landowners are re-introducing selected species into the area. Thus, managers require knowledge on how to implement practical guidelines for best-practice grazing management. This study investigates, firstly, the relationship between plants and animals. This included seasonal assessment of seed germination from dung of bontebok and eland; the effect of stocking rates on plant palatability (crude protein, crude fibre, crude fat, moisture, tannin and mineral) of herbage was studied with the aim to understand how palatability influences herbivore forage decisions. Secondly, this study looked at how stocking rates influence soil nutrients (nitrogen, phosphorus), and others soil properties such as pH and soil moisture.

The distribution of alien grasses was facilitated by grazers. About 58 % of grasses germinated from the dung of eland and Bontebok were alien species. Additionally, there was significant variation in palatability related to grazing pressure and plant maturity between sites and over seasons. Grasses on the high grazing site had higher carbohydrate (3%-5% higher) and protein content (1%-5% higher) than at the least grazed site. Mature grasses contained less water (10%-20%), but no obvious variation in tannin concentration than immature grasses. However, species such as *Ficinia sp.* showed variations with grazing pressure and maturity. *Ficinia sp*. on the high grazing site had higher tannin concentration (5mg/ml-22mg/ml) and crude protein (4%-9%) than at the least grazed site. When the plant ages, tannin concentration increase (ranging from 15% to19% higher). Two types of plant were recoreded according to their chemical response following grazing pressure. These types are 1) plants that are grazing tolerant and which produce more carbohydrate when grazed and 2) plants that are grazing intolerant under high grazing pressure and which produce chemical defence compounds such as tannin to deter herbivores attacks. The results indicate that in fynbos and renosterveld, the relationship between preference and plant chemical compounds is not consistent since no

patterns emerged to explain what compounds drive preference. A combination of chemical compounds may be the reason for the selection by the grazers; alternatively, other compounds not included in the study may influence the forage selection by an herbivore.

The second part of the study showed that stocking rates appeared to have a significant effect on soil properties investigated. Soil moisture was significantly affected by the stocking rate in autumn. The high grazing intensity site had the lowest soil moisture especially in autumn (10% lower than the control site), likely due to heavy trampling and soil compaction. pH was the lowest at the high grazing intensity site in all seasons compared to the control site. Likely reasons were the high deposition of nitrogen through dung and urine deposition, high removal of basic cations and animal exportation through hunting activities. Lastly, grazing maintains inorganic nitrogen at stable levels regardless of seasonal changes and increases the concentration of phosphorus especially under high grazing pressure compare to less grazed sites.

The grazing dynamics of Swartland Shale Renosterveld - Swartland Alluvium Fynbos mosaic system are complex and multifaceted. Farmers need to pay attention to the nutritional status of plant species grazed to know whether they meet the nutritional requirements of the game in the area. Overstocking should be avoided in this system as it triggers the production of tanniferous compounds that could decrease the survivorship of herbivores. Moderate grazing 0.09 LAU/ha pressure provides the best stocking rates for effective grazing management.

# OPSOMMING

Vir suksesvolle weidingsbestuur is dit noodsaaklik om die interaksie tussen herbivore, plantvoedingstowwe en grondeienskappe te verstaan. Van besondere belang is plantsmaaklikheid en herbivore se weidingsvoorkeure. Hierdie aspekte, wat die fokus van hierdie tesis is, is bestudeer in ‘n Swartland Shale Renosterveld en Swartland Alluvium Fynbos-mosaïek in die Wes-Kaap Provinsie van Suid-Afrika. Hierdie plantegroei word as kritiek bedreigd geklassifiseer weens die transformering van sy landskap ten gunste van landbou-aktiwiteite en stedelike vestiging.

Pre-koloniale herbivoor vertebrata is teen 1700 deur jagters uitgeroei, wat gelei het tot min kennis oor die vroeë dinamiek van die plantegroei. Wildsboere en grondeienaars is egter besig om geselekteerde spesies in die area te hervestig. Bestuurders moet dus weet hoe om praktiese riglyne vir beste-praktyk weidingsbestuur te implementeer. Hierdie studie ondersoek eerstens die verhouding tussen plante en diere. Dit sluit seisoenale evaluering van saadontkieming uit die mis van bontebokke en elande in; die effek van veegetalle op plantsmaaklikheid (ruproteïen, ruvesel, ru-vet, vogpeil, tannien en minerale) van die weiveld is bestudeer om vas te stel hoe plantsmaaklikheid herbivore se weidingsbesluite beïnvloed. Tweedens het die studie die invloed van veegetalle op grondvoedingstowwe (stikstof, fosfor) ondersoek, asook ander grondeienskappe soos pH en grondvogpeile.

Die verspreiding van uitheemse grasse is deur weidende diere gefassiliteer. Ongeveer 58% van alle grasse wat uit die mis van elande en bontebokke ontkiem het, was uitheemse spesies. Verder was daar beduidende variasie in plantsmaaklikheid verwant aan beweidingsdruk en plantvolwassenheid tussen verskillende persele en oor seisoene. Grasse op die hoogs beweide persele het 3%-5% hoër koolhidraatinhoude en 1%-5% hoër proteïeninhoude gehad as die minder beweide persele. Volwasse grasse het 10%-20% minder water bevat as onvolwasse grasse, maar het nie in terme van tannienkonsentrasie van die onvolwasse grasse verskil nie. Spesies soos *Ficinia sp.* het variasies getoon met beweidingsdruk en volwassenheid. *Ficinia sp*. het op die hoog-beweide perseel ‘n hoër tannienkonsentrasie (5mg/ml-22mg/ml) en meer ruproteïen (4%-9%) gehad as op die minste beweide perseel. Wanneer die plant verouder, verhoog die toename in tannienkonsentrasie (met tussen 15% en 19%). Twee tipes plante is aangeteken volgens hul chemiese response ná beweidingsdruk. Hierdie tipes is 1) plante wat beweidingstolerant is en wat meer koolhidrate produseer wanneer hulle as weiding dien en 2) plante wat onder hoë beweidingsdruk beweidingsintolerant is en wat chemiese verbindings

soos tannien produseer om herbivooraanvalle af te weer. Die resultate dui aan dat die verhouding tussen voorkeur en plante se chemiese verbindings nie konstant bly in fynbos en renosterveld nie, aangesien geen patrone na vore getree het wat kon verklaar watter verbindings bepalend is vir voorkeur nie. ‘n Kombinasie van chemiese verbindings mag die rede wees waarom die herbivore sekere plante verkies; alternatiewelik mag ‘n herbivoor se plantseleksie beïnvloed word deur chemiese verbindings anders as dié wat in hierdie studie ondersoek is.

Die tweede deel van die studie het aangetoon dat veegetalle blyk ‘n beduidende invloed te hê op die grondeienskappe wat ondersoek is. Grondvogpeile is in die herfs beduidend beïnvloed deur die veegetalle. Die perseel met die hoë beweidingsintensiteit het die laagste grondvogpeil gehad, veral in die winter (10% laer as dié van die kontrole-perseel), waarskynlik weens erge getrappel en grondkompaktering. Vergeleke met die kontrole-perseel was pH die laagste op die perseel met die hoë beweidingsintensiteit, in alle seisoene. Waarskynlike redes hiervoor is die hoë neerslag van stikstof deur mis- en uriene-neerslae, hoë verwydering van basiese katione en dierevervoer wat deur jagaktiwiteite teweeg gebring word. Laatstens behou weiding anorganiese stikstof teen stabiele vlakke ongeag van seisoenale veranderinge en toenames in die konsentrasie van fosfor, veral onder hoë beweidingsdruk vergeleke met minder beweide persele.

Die weidingsdinamiek van die Swartland Shale Renosterveld - Swartland Alluvium Fynbos-mosaïeksisteem is kompleks en veelvlakkig. Boere behoort aandag te skenk aan die voedingstofstatus van die plantspesies wat as weiding dien, sodat hulle kan weet of die voedingsbehoeftes van die wild in die omgewing bevredig word. Die aanhou van te veel vee in hierdie sisteem behoort vermy te word aangesien dit as sneller dien vir die produksie van tannienbevattende verbindings wat die oorlewingsvermoë van herbivore kan verlaag. Matige beweidingsdruk (0.09 LAU/ha) bied vir effektiewe weidingsbestuur die beste veegetalle.

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# THESIS STRUCTURE

The thesis consists of five chapters that focus on answering the questions regarding the variation of plant and soil characteristics under different grazing intensities and over four seasons in a fynbos-renosterveld mosaic. Chapter 1 deals with the history and the ecology of the study and provides the background for the study. Chapter 2 is a literature review that explores plant chemical responses and soil properties in relation to grazing pressure and seasonal variation. Hypotheses and predictions are formulated based on these two chapters. Chapters 3 and 4 deal with the experimental component, providing the answers and the predictions through statistical analysis of data. Finally, chapter 5 summarises the results of the previous chapters and provides recommendations for farmers and landowners, as well as future research prospects.

The thesis style follows that of the African Journal of Ecology.

# Chapter 1: General Introduction

## 1.1 Study context

Plant-animal interactions have long been the focus of research across the world. Nevertheless, in the lowland areas of the Western Cape of South Africa, the understanding of these interactions, especially plant-herbivore interactions, is still sparse. The high degree of transformation of the landscape due to anthropogenic activities in the lowlands has confined herbivores to restricted areas. In addition, the lack of historical records of the effect of the large mammalian herbivores on the vegetation is an acute gap in knowledge of the role played by these large herbivores in the ecosystem. This study was conducted in a Swartland Shale Renosterveld-Swartland Alluvium Fynbos mosaic in the lowlands of the Western Cape of South Africa. Specifically, two sites with different stocking rates (medium and high) as well as a control site were selected to provide an understanding of the interactions of large game with vegetation and soil properties. Information for this area is available on vegetation dynamics and successional patterns (Walton, 2006) as well as the restoration processes (Midoko-Iponga, 2004; Memiaghe, 2008). However, the relationship between large indigenous game and plant and soil properties is still yet to be discovered.

### *History and ecology*

Along with Fynbos, which is most common on upland sandstone substrates, lowland renosterveld is one of the dominant vegetation types in the Cape Floristic Region (Von Hase *et al*., 2003). The lowland Renosterveld is usually restricted to the richer fine-grained soils compared to fynbos, although it often occus adjacent to fynbos which it shares a few species (Goldblatt & Manning, 2002; Krug, 2004). It is well known for its spectacular diversity of geophytes (Boucher, 1981; Proches *et al.*, 2005), which in the past could play an important role for human subsistence (Avery, 1981), and species such as microphyllous Asteraceae, which form a dense shrubland. The rich herbaceous understory that appears after fire is one of its distinctive characteristics (Goldblatt & Manning, 2002). The lowlands have been used for grazing by livestock belonging to the Khoi-Khoi pastoralists for centuries and later by the Dutch settlers (Hoffman, 1997; Kemper, 1997), as they were easily accessible and more productive than the uplands (Hoffman, 1997). The arrival of European settlers had a profound impact in two ways: the settlement of a pastoral economy and the reduction or elimination of indigenous game (Hoffman, 1997). However, the historical and archaeological evidence

suggests that the nomadic seasonal movement of the Khoi-khoi maintained veld in good condition (Hoffman, 1997), compared to the impact of the establishment and the expansion of permanent Dutch settlement (Avery, 1981). Until today, these lowlands are under severe anthropogenic pressure.

The early dynamics of the lowlands are barely known and fynbos was suggested to be more common in the area compared to the renosterveld (Low & Rebelo, 1996). Fire, which is an important factor in this ecosystem (Krug *et al*., 2004), was used by Hottentot tribes or nomadic Khoisan to stimulate vegetation regrowth for grazing purposes (Boucher, 1981). This was later (after 1652) utilized by the Europeans, creating a huge destruction of the foreland vegetation through the quest for more intense levels of grazing and agricultural production (Boucher, 1981). During the early and middle European settlement period, a wide reduction of large herbivores and mega-herbivores occurred (Skead, 1980), coupled with an introduction of alien plants (Hoffman, 1981). This contributed to a disruption of the ecological processes in the ecosystem, and leading to further transformation of the region.

***Large herbivores and their roles in the Cape Province***

Approximately ninety species of the total southern African fauna of about 280 species occurred in the South Western Cape (Bigalke, 1979). Skead (1980), relating to the historical incidence of mammals in the Cape Province before European settlement, suggested that in the past, the Cape Province used to sustain a wide variety of indigenous game species, among them, black rhinoceros (*Diceros bicornis*), elephant (*Loxodontana africana*), eland (*Taurotragus oryx),* rhebok (*Pelea capreolus*), red hartebeest (*Alcelaphus buselaphus)* and bontebok *(Damaliscus dorcas dorcas*). However, for the time the Cape was colonized, the historical records have not given clues to the full distribution of species (Skead, 1980). Some species may have never been recorded, identified or classified, creating a gap in the knowledge on the ecological importance of these species. Information is available on how large herbivores impact on plant community structure and dynamics (Hester *et al*., 2006), how they effect plant diversity (Ward, 2006), on physical disturbance (Hobbs, 2006) and the role they play in the process of nutrient cycling (Pastor *et al.*, 2006). Based on this knowledge, speculations can be made on the role played by large herbivores in the Cape lowlands before European settlement.

Historical records suggest that the introduction of domestic livestock and agriculture has profoundly affected the ecosystem stability of the lowlands (Hoffman, 1981; Avery, 1981;

Krug *et al*., 2004; Krug, 2004). Grazing leads to an equal distribution and abundance of species (Krug *et al*., 2004), leading to the conclusion that the removal of large herbivores from that area lead to species such as renosterbos (*Elytropappus rhinocerotis*) to become dominant. Rebelo (1992) reported that large mammals played a great role in non-fynbos vegetation where they were apparently abundant. Herbivores, in the past, could thus sustain vegetation abundance and stability in the lowlands. In addition, large herbivores might have dispersed indigenous seed via their dung. Shiponeni and Milton (2006) found that large mammalian herbivores such as eland were major dispersal agents of seed through the veld. In addition, large herbivores could have contributed to nutrient recycling in the area, through dung and urine deposition (McNaughton *et al*., 1988), as well as their own body decomposition after death (Pastor *et al*., 2006). Nevertheless, Rebelo *et al*. (2006) state that the topic of the influence of large herbivores in fynbos ecosystems has long been ignored.

### 1.2 Conservation issues

Today, the fynbos-renosterveld mosaic of the lowlands is classified as critically endangered (Rebelo *et al*., 2006). Less than twenty-five percent of the original extent remains (Rebelo *et al*., 2006). The causes of the transformation of the vegetation are multiple: vineyards, olive orchards, pine plantations and urban settlement (Greig & de Villiers, 1982; Krug, 2004; Rebelo *et al*., 2006). This situation contributed to fragmentation of the vegetation with the remaining renosterveld fragments depicted in Figure 1 (von Hase *et al.,* 2003). Hall (1981) reported that the conservation standards of the Western Cape lowlands have been insufficient in meeting the criteria for ensuring the survival of species. For instance, the geometric tortoise (*Psammobates geometricus*), which depends on the survival of the coastal lowland vegetation, is now confined to less than 4 % of the vegetation (Greig & de Villiers, 1982). Although the Rio Convention proposes that at least 10% of each vegetation type should be protected for pristine or near pristine use (Low & Rebelo, 1996), this is not the case for lowland renosterveld. Von Hase *et al*. (2003) reported that less than 2 % of this vegetation is formally protected. In comparison to South Coast Renosterveld, West Coast Renosterveld has been transformed over a longer period with an estimated 80 000 ha cultivated between 1918 and 1990 (Kemper, 1997).

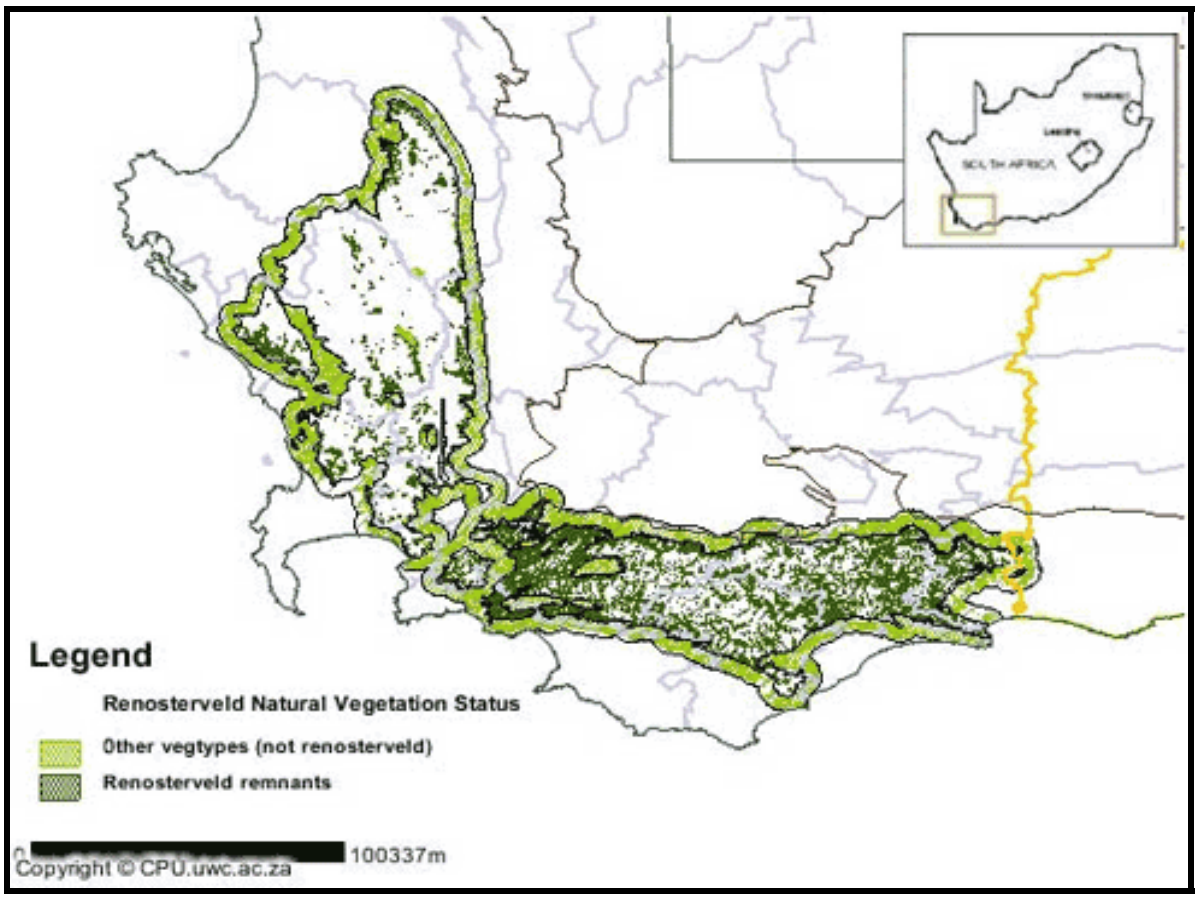


Figure 1: Cape Lowland Renosterveld Vegetation Remnants, Western Cape, South Africa.
(von Hase *et al.,* 2003, *source :* http://bgis.sanbi.org/clr/vegetationRemnants.asp)

Due to its sparse vegetation cover, the lowlands are likely to be invaded by alien grasses (Milton, 2004). Vlok (1988) reported that alien grasses are able to establish effectively in the lowlands, where they become a threat to indigenous flora. In addition, there is also the presence of alien invasive animals such as feral pigs that disturb the vegetation through their search for geophytes (Krug *et al*., (2004); Mike Gregor and Steve Mitchell, personal communication), facilitating invasion by alien species and threatening restoration attempts.

### 1.3 Rationale and objectives

Since the survival of many species depends on the existence of the lowlands and the habitats they provide (Greig & de Villiers, 1982; Baard, 1995), coupled with its uniqueness worldwide, an investigation of the remaining fragments is crucial. Compared to fynbos ecosystem processes, lowland renosterveld is poorly documented. Previous studies focused on the geometric tortoise (*Psammobates geometricus*) (Baard, 1995; Balsamo *et al.,* 2004; Henen *et al*., 2005), habitat fragmentation (Kemper *et al*., 1999; Donaldson *et al*., 2002), response to

disturbance such as fire and grazing (Beukes, 1987; Midoko-Iponga, 2004), ploughing (McDowell & Moll, 1992; Walton, 2006) and seed dispersal (Shiponeni & Milton, 2006). Of particular interest here is the effect of browsing and grazing on the vegetation, as indigenous large herbivores are being re-introduced on game farms and into nature reserves, and farmers and conservationists require management information.

Damage sustained through herbivory often changes the chemical composition of plants (Steinke & Booysen, 1968; Wolfson, 1999). Moreover, grazing has significantly contributed to the evolution and maintenance of diversity in plant communities (Cowling *et al*., 1983), and modifies soil properties (McNaughton *et al*., 1992; McNaughton *et al*., 1997). The study aims to provide information to the grazing management of a lowland fynbos-renosterveld mosaic by investigating plant and soil attributes that interact with grazing intensity and seasonal variation. This study involves two mammal species with historical presence in the Cape Province during the early European settlement (Skead, 1980), eland (*Taurotragus oryx*), which is a mixed feeder, and bontebok *(Damaliscus dorcas dorcas*) exclusively a grazer (Skinner & Smithers, 1990). The following questions are addressed:

1. How does herbivory by large game impact on plant palatability (i.e. plant chemical compounds) across three different grazing intensities?
2. How does grazing intensity influence forage palatability and hence their preference by indigenous game?
3. How do soil properties vary between different grazing intensities?

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# Chapter 2: Effect of grazing on plant physiological traits, and soil chemical properties

## 2.1 Introduction

Plant-animal interactions are an important focus in ecology, involving complex relationships with a wide range of patterns. The understanding of these patterns is a fundamental tool for grazing management (Migongo-Bake & Hasen, 1987; Gordon *et al.,* 2004; Cash & Fulbright, 2005). Of significance are the physiological attributes that plants express when they are experiencing different grazing intensities, or grazing histories (Oesterheld & McNaughton, 1988). These attributes (i.e. plant defence mechanism systems) are complex and their understanding is currently limited (Belovsky & Schmitz, 1994; Schroder, 1998; Zangerl, 1999; Underwood, 2000; Agrawal *et al.*, 2002). The field is therefore open for further investigation.

Studies on plant and animal interactions have led to a broad understanding of animal "forage preference" and "plant palatability". The understanding and distinction of both terms is of importance to the knowledge of grazing management, especially for vegetation such as that of fynbos and renosterveld, where very little is known about grazing. Heady (1964) defined forage preference as the behavioural selection by an animal, and plant palatability as those characteristics and conditions which stimulate a selection response by animals. Vallentine (1990) defined preference as the selective response made by an animal to plant. This selection is essentially behavioural. Palatability, according to Vallentine (1990), is a combination of characteristics that stimulate animals to prefer one type of forage to another. Thus, in the field of feeding ecology, palatability helps to understand and evaluate the forage habit of an animal, since it is mainly based on the quantitative value of nutrient content of the forage plant. Palatability then, allows the scientist to make conclusions on the diet composition of an animal and therefore to understand the avoidance or acceptance of herbage. Vallentine (1990) highlighted the fact that preference and palatability are interconnected. This is the reason why plant palatability is known as one of the major factors affecting forage preference (Heady, 1964).

In fynbos and renosterveld vegetation types, where little attempt has been made thus far to understand the impact of large game on plant palatability, the question whether preference of

herbage will be governed by patterns such as the physical accessibility of the plant material, the physiological adaptation of the animal, the acceptability of the plant material and the surrounding conditions are pertinent (Owen-Smith, 1999).

To evaluate forage preference, investigations have been conducted on various aspects including seasonal variation (Bedell, 1968; Gray *et al.*, 2007), species morphology (McAdam & Mayland, 2003), and theoretical models (e.g. Nudds, 1980). Mathematical equations such as the relative preference index (Krueger, 1972), forage preference indices (Loehle & Rittenhouse, 1982), Ivlev electivity index (Ivlev, 1961), or the rank preference index proposed by Johnson (1980) have been used to evaluate forage preference. Some of them are based on various attributes that depend on environmental factors and investigator viewpoint. As a starting point, the method proposed by Johnson (1980) seems the most appropriate for this study, as it does not require the analysis of attributes such as germination of seed from the dung, or stomacal epidermic layer identification of plant remains found in dung samples.

So far, four characteristics have been identified that improve plant palatability. These characteristics are: high protein content, low crude fibre content or non-fibrous plants, high plant moisture content and low anti-feedant chemical compounds (Vallentine, 1990; Launchbaugh, 1998; Van Hoven, 2002). For example, in Anysberg Nature Reserve, in the Little Karoo of South Africa, Farmer (2005) investigated the use of the landscape by indigenous herbivores. The palatability scores of three plant groups (high protein and mineral; high sugar plant; high ether extract plants) were evaluated. Groups of plants with high protein and high mineral content correlated with high palatability, whereas groups with high ether extract were avoided. She also found that palatability increased with a decrease in fibre. In the Mountain Zebra National Park (MZNP) in South Africa, Watson and Owen-Smith (2000) demonstrated that eland browsed mainly woody species with lower fibre content. Although it is widely accepted that animals select species with low fibre and high crude protein content (Bryant & Kuropat, 1980; Hart & Hoveland, 1989), some species shift or mix their diet to compensate their daily or seasonal needs (Migongo-Bake & Hansen, 1987). Nevertheless, little is known about the ability of large herbivores to cope with seasonal changes in plant compounds in fynbos and renosterveld vegetation types.

The main characteristics decreasing palatability of plants are fibrous forage plants, high levels of anti-feedant chemicals such as tannin, and low plant protein content (Vallentine, 1990; Launchbaugh, 1998). For example, Fashing *et al*. (2007) reported that fibre played a much

greater role compared to protein in the selection of food items by guereza (*Colobus guereza*) in Kakamega, Kenya. In fact, all food items with high fibre content were simply avoided, and the leaves ignored by guerezas were found to have high-condensed tannin content.

Tannin is a compound well known to reduce enzyme activities by binding with proteins and making it unpalatable for herbivores (Hodkinson & Hugues, 1982; Cooper & Owen-Smith, 1985; Bryant & Raffa, 1995). Nevertheless, to cope with secondary compounds, herbivores mix their diet to balance the quantity between nutrient rewards and anti-feedant content (Villalba *et al*., 2004) or by secreting tannin-binding salivary proteins (Shimada, 2006).

**2.2 Plant chemical responses to grazing**

Under different grazing intensities, forage plants can change their chemistry either negatively or positively (Paige, 1992). As a negative response, plants under grazing pressure can synthesize anti-palatable chemicals to deter herbivore attacks, whereas a positive response is the replacement of tissue lost by herbivores by resource allocation of nutrients (Danckwerts, 1989; Vallentine, 1990; Oesterheld & McNaughton, 1991; Juenger & Lennartsson, 2000; Juenger *et al*., 2000; Hester, 2006).

Under grazing pressure, the negative response manifests in qualitative or quantitative defences. Qualitative defences are compounds such as alkaloids, cyanogenic glucosides, non-protein amino acids, cardiac glycosides and glucosinolates, which are toxins (Caughley & Sinclair, 1994; Van Hoven, 2002). These compounds affect herbivore activity in minute concentrations and are present in low quantities (Lambers *et al*., 1998). Quantitative defences, such as tannin, are "phenolic compounds" and are able to reduce the digestibility or palatability of the food plant (Lambers *et al*., 1998).

In the savanna vegetation of South Africa, Cooper *et al*. (1988) realized that the diet of the kudu and impala was extremely affected by the concentration of condensed tannin, even though the nutrient content of the selected food was relatively acceptable. Martin and Martin (1982) stated that tannin is an important aspect in theories on plant-animal interactions. Two classes of tannin have to be distinguished (Hodkinson & Hugues, 1982): the condensed tannin and the hydrolyzed tannin. This study takes into consideration only the condensed tannin which is from here on is referred to simply as tannin.

The response of plants to herbivory goes beyond the scope of the biosynthesis of secondary metabolite compounds because plant species are an association of various chemical constituents such as protein, mineral, fat, water and carbohydrate (Bailey, 1984). The amount of each constituent is taxonomy-dependent as well as seasonally dependant (Barth & Klemmedson, 1986). Herbivory can influence the physiology of the damaged plant through relocation of nutrients to maintain its fitness. For instance, instead of being repellent or decreasing productivity, the plant can be tolerant. Augustine and McNaughton (1998) describe tolerance as the survivorship and competitive abilities of a plant.

Moderate grazing promotes the productivity of grassland and increased nitrogen phytomass concentration (McNaughton, 1993; Leriche *et al*., 2003). Augustine and McNaughton (1998) stated that after herbivory attacks, plant relative growth rate (RGR) could respond in three ways: Firstly, it can be inhibited; this means that there is no response at all from the grazed plant. Secondly, it can remain constant as before the event, meaning that the growth rate shows no fluctuations and lastly, it can increase after herbivory. Steinke and Booysen (1968) investigated the re-growth and utilization of *Eragrostis curvula* reserves at various levels of defoliation, and realized that to compensate for the loss from herbivory, the forage plant drew nutrients from carbohydrate reserves. Polley and Detling (1988) concluded that grazing promotes growth and biomass accumulation.

In order to obtain a better understanding of the effect of herbivory on plants, farmers and landowners, in a vegetation where the knowledge of large game is still sparse, need to be aware that patterns of plant-animal interaction are complex and involve multiple factors that may depend on grazer behaviour, stocking rate, and also on the species grazed (physiological ability, age of the plant). A number of studies on veld quality have been conducted in the Northern Cape, however, as the environmental factors there are very different from those in the winter rainfall region of South Africa, they are of limited merit for fynbos and renosterveld vegetation types.

Plant age, especially maturity, decreases plant protein and increases crude fibre and carbohydrate content (Khan *et al*., 2007; Ramirez-Tobias, 2007). For example, in the northern savanna of South Africa, the quality of browse species, especially the protein content of shrubs and trees, decreases as the plant ages, while crude fibre increases (Groenewald *et al.*, 1967). Georgiadis and McNaughton (1990) stated that in the Kajiado district of southern

Kenya, there was a decline in protein content, whereas the carbohydrate content increased in savanna grasses as the growing season progressed.

To cope with this seasonal variation of the environment, herbivores find their way around by shifting their diet (Bahamonde *et al*., 1986; Tomlinson, 1980), or secreting proteins that neutralise the effect of tannin (Owen-Smith, 1999). For example, in northern Kenya, cattle, goat and sheep were observed to shift their diet between the green and the dry season (Migongo-Bake & Hasen, 1987).

### 2.3 Impacts of grazing on soil nutrient status

Soil properties are recognized to affect plant chemical attributes (Chunlong *et al.*, 2008). In agriculture, the understanding of the soil properties is crucial for plant productivity (Phillips-Howard & Lyon, 1994). In South Africa, the growth rate of common species in acacia savanna is reduced in nutrient poor soils, whereas in soils rich in nutrients, plants grow faster (Bryant *et al*., 1989). This is correlated with the common generalization that growth rate is reduced under nutrient deficiency (Evans, 1996). The soil is a living entity that provides habitat for a wide range of organisms (Coleman *et al*., 2004), and is the basis from which plants take root, stability and all mineral elements vital for their growth. For centuries, in the Western Cape region of South Africa, soil has been used in farming to fulfil anthropogenic needs (Fairbanks *et al*., 2004; Krug *et al*., 2004; Rebelo *et al*., 2006). Soil properties are important for herbivores because in a nutrient-poor environment, plants are not able to grow efficiently and healthy (Fleming, 1973). Thus, animals feeding in such environments are exposed to a poor diet. Herbivores under poor feeding conditions would thus suffer from nutrient deficiency (Butler & Jones, 1973). For instance, in South Africa, Schmidt and Snyman (2002) reported that in the minerally deficient western and the southern coastal belt regions, white muscle disease symptoms were recorded in mammalian herbivores, indicating a deficiency of selenium.

The presence of herbivores such as domestic livestock or indigenous game, influence or modify soil chemical properties in a particular system (Xu *et al.*, 2007). In systems such as the fynbos and renosterveld in the Cape Floristic Region of South Africa, game farming is on the increase, and the interaction effect between soil properties and grazing is poorly documented, especially under differing stocking rates. Therefore, it is crucial to investigate the effect of large herbivores on soil chemical properties in order to understand the effect of

stocking rates on plant chemical properties. This study investigates the following soil properties: pH, soil moisture content, carbon to nitrogen ratio, nitrogen and available phosphorus.

### *Soil pH*

Soil pH is a measure of the alkalinity or acidity of the soil solution. It controls the nutrient availability of soil and is affected by the water regime and the soil organic matter decomposition through the release of organic acids (Bardgett, 2005). It has been shown that when nutrients are washed away by an increase in water input, this causes a decrease in pH (Black, 1968; Bohn *et al*., 1979). Furthermore, pH has the ability to influence the litter decomposition of organic matter (i.e. nitrate release is more rapid in neutral soil than in acid soil). Additionally, neutral soil increases the decomposition rate, while acid soil decreases it (Etherington, 1975; Bohn *et al*., 1979). Soil pH can be affected by different grazing intensities (Walters & Martin, 2003). For example, when comparing the effects of three grazing intensities on soil chemical properties, Mapfumo *et al.* (2000) found that soil pH was lower under heavy grazing than under medium and light grazing. They explained that the increase of $NH_4^+N$ from dung and urine deposition could have been the cause of the lower pH value under the high grazing intensity. In relatively nutrient poor soils of as renosterveld (although they are nutrient-rich compared to fynbos soils), it is yet to be discovered whether high grazing pressure will produce the same results.

### *Soil moisture*

Water is the component with which nutrients are taken from the soil to the root system of plants. Its depletion generates a decline in nutrient uptake and triggers a change in the physiological condition of plants (Etherington, 1975). For example, Katjiua and Ward (2006) found that under low soil moisture, seedlings of *Terminalia sericea* had higher condensed tannin concentration than under a high water treatment. Soil water content further affects soil organic matter decomposition (Coleman *et al*., 2005), for example, under dry conditions, soil decomposition of organic matter is reduced (Jenkinson, 1981). However, under grazing pressure, through herbivore trampling, soil moisture is affected. Studies have shown that soil moisture content decreased with an increase in grazing pressure (Dormaar *et al.*, 1989; Walters & Martin, 2003), and this effect was more pronounced under moist conditions (Warren *et al.,* 1986).

### *Soil carbon to nitrogen ratio*

The amount of carbon relative to the amount of nitrogen in the soil determines the capability of bacteria to decay organic matter into mineral matter (Ruess & McNaughton, 1987; Lavelle & Spain, 2001). This ratio takes decades to vary significantly, as decomposition is a relatively slow process. Soil with a high carbon to nitrogen ratio has a low decomposition rate, whereas soil with a low carbon to nitrogen ratio has a high decomposition rate (Ruess & McNaughton, 1987). However, carbon to nitrogen ratios can vary with rainfall and temperature amongst others (Snowdon *et al.*, 2005), as rainfall provides more water to micro-organisms involved in the process of decomposition of organic matter, and temperature increases their activity.

### *Soil nitrogen (ammonium and nitrate)*

Nitrogen is of importance to all life forms on earth because it constitutes the building blocks of protein for animals and plants and is the limiting factor in plant growth. In the soil solution, two categories of nitrogen can be classified according to their nature: organic nitrogen and inorganic nitrogen (Satchell, 1974; Lavelle & Spain, 2001). Organic nitrogen is a building block of living organisms while inorganic nitrogen is a product of mineralization after decomposition of organic matter. For the purpose of the study, I focus on mineral nitrogen.

Inorganic nitrogen is the product of decomposition of organic matter by micro-organisms (Gyllenberg & Eklund, 1974). Herbivores, through the excretion of dung and urine, enhance mineral nitrogen in the soil (Ruess & McNaughton, 1987; McNaughton *et al.*, 1997). In the Serengeti National Park, Tanzania, McNaughton *et al*. (1997) found that the production of soil nitrogen after addition of the enzyme urease was positively correlated with the grazing intensity (McNaughton *et al.,* 1997). Soil urease is of ecological importance in the grazing ecosystems as it converts urea to inorganic compounds and leads to an increase in mineralization. Herbivores, therefore, promote and enhance the mineralization process in the soil (Seagle *et al.*, 1992).

Under natural conditions, mineral nitrogen in the soil is present as ammonium nitrogen ($NH_4^+N$) or nitrate nitrogen ($NO_3^-N$) (Haynes & Goh, 1978). The transformation of organic nitrogen to ammonium is called ammonification and the transformation of ammonium to nitrate is called nitrification. These two processes are not linear and could under specific conditions progress differently. For instance, nitrification is much more sensitive to low

temperature than ammonification. This implies that at low temperatures, nitrification could be stopped while ammonification still occurs (Black, 1968). Additionally, under a lack of aeration, especially under water-logged situations, nitrification could be stopped, which is not necessarily the case for ammonification (Black, 1968). Finally, the nitrifying bacteria decrease their activity when the soil solution becomes more acidic (Etherington, 1975).

***Phosphorus***

Phosphorus is involved in a multitude of biological processes and constitutes a limiting factor to plant growth (Bardgett, 2005). For instance, Chapin and McNaughton (1989) studied the lack of compensatory growth under phosphorous deficiency in grazing adapted grasses. They found that under phosphorus deficiency, there is a feed-back reduction in biomass of all plant parts for all species studied. In the soil solution, phosphorus is available to plants in the form of orthophosphate $H_2PO_4^-$ or $HPO_4^{2-}$ (Lavelle & Spain, 2001). Phosphorus availability decreases in acidic soil and becomes more available to plants at a pH of about 6 to 7, which is the neutral point (Bardgett, 2005). Herbivores provide phosphorus to the soil through faeces (Wilkinson, 1973). In the Tallgrass Prairie National Reserve, Kansas**,** it has been shown that as grazing intensity increased, the phosphorus content in the soil solution increased as well (Walters & Martin, 2003).

Environmental conditions related to abiotic stress influence plant physiology (Owen-Smith & Cooper, 1987; Chapin & McNaughton, 1989; Georgiadis *et al.,* 1989). In resource rich environments, plants have lower amounts of chemical defensive compounds, thus they are subjected to a greater rate of herbivory (Coley *et al.,* 1985), whereas plant species growing in nutrient-poor environments decrease their growth rate and increase the production of secondary metabolic compounds (Chapin & McNaughton, 1989). It could therefore be expected that plant species growing in the relatively nutrient poor renosterveld soils will increase the amount of secondary compounds, e.g. tannin, to deter herbivores in order to cope with different grazing pressures that naturally will not occur.

## 2.4 Conclusions and hypotheses

This literature review reveals that interactions of plants, animals and soil properties are complex and multifaceted. Most of the investigations agree that herbivores select species with high nutrient quality and low fibre content (Watson & Owen-Smith, 2000), and production of secondary metabolites is damage-dependant (Zangerl, 1999). Additionally, plant fitness relies

on soil properties, while animal fitness relies on plant nutrient content (McNaughton & Georgiadis, 1986; Ratliff, 1986; Ridder *et al*., 1986; Bryant *et al*., 1989; Evans, 1996). There are uncertainties about the response of species growing in renosterveld and fynbos soils because few studies have emphasised this aspect. Most of the studies with regards to this were done in the northern Transvaal bushveld (Cooper & Owen-Smith, 1985; Owen-Smith & Cooper, 1987; Cooper *et al*., 1988), and the Karoo veld (Milton, 1994; Vorster, 1999; Wolfson & Tainton, 1999), of South Africa. The question, whether results observed in those vegetation types will be the same for fynbos and renosterveld vegetation types, is unresolved. Based on the present chapter the predictions of the plant chemical responses and soil properties are:

1. Plant species with high protein content, low fibre content and tannin concentration will be the most palatable.
2. Herbivores will demonstrate a preference for species with low levels of chemical antifeedants.
3. Grasses and shrubs found at the high grazing intensity site will contain a higher amount of antifeedants.
4. Forage plant of the medium grazing intensity will have the higher tolerance rate through the high production of carbohydrate.
5. Soil will be richer in nutrients where grazing intensity is higher.
6. pH values will be lower in winter as nutrients will be washed away by rainfall, whereas moisture will be the highest in winter at all sites.
7. Moisture will be the highest, while pH will be lowest on the high grazing site.
8. The carbon to nitrogen ratio, as well as levels of phosphorous and available nitrogen will be higher at the high grazing site in comparison to the low and medium grazing sites due to the high nutrient input.
9. Moisture will be the main factor influencing the concentration of the nitrogen availability in the soil.

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# Chapter 3: Forage preference and plant palatability across a grazing gradient in an Alluvium Fynbos-Renosterveld mosaic

## 3.1 Introduction

Plant-animal interactions are of relevance to the management of herbivore effects on vegetation (Sankaran & McNaughton, 2005). In natural environments, herbivores are surrounded by an apparent oversupply in food. However, whether a particular food item is grazed by a herbivore is affected by the change not only in terms of quantity, but also quality of the herbage (Van Hoven, 2002). Of particular interest are the chemical compounds that plants have evolved to deter herbivores. These compounds are often diverse and their effects are still subject to discussion (Karban & Myers, 1989; Bryant *et al*., 1992; Van der Heyden & Stock, 1999). In the Karoo bio-region of South Africa, these compounds are reported to play an important role in palatability of the herbage (Van der Heyden & Stock, 1999). Historically, large indigenous game species were abundant in the Western Cape of South Africa (Skead, 1980). Since European settlement, however, game declined in diversity and abundance (Skead, 1980; Krug *et al*., 2004). At the same time, vegetation types such as renosterveld and alluvium fynbos have been transformed through a number of human activities, and today only highly fragmented patches remain, often restricted to ecotonal areas not suitable for agricultural production. In an effort to conserve the remaining patches, alternative land-uses such as game farming and ecotourism are currently being explored. However, to manage biodiversity effectively under these alternative land uses, an understanding of the impact of large game on vegetation, including plant chemical attributes as well as how these in turn impact on herbivore diet selection, is required.

It is widely acknowledged that plant species with a high protein and low fibre content are palatable, while plants with low protein and high fibre content are less palatable (Vallentine, 1990). Plant palatability can be described as those plant characteristics and conditions which stimulate a selection response by herbivores, while preference is the behavioural selection of an animal (Heady, 1964). Palatability and preference are interconnected (Vallentine, 1990), in other words each chemical compound affecting palatability will also affect preference. For example, in the Nylsvley Nature Reserve situated in the northern Transvaal bushveld in South Africa, Cooper and Owen-Smith (1985) investigated the palatability of 14 woody species for greater kudu (*Tragelaphus strepsiceros*), impala (*Aepyceros melampus*) and goats. The results

showed that plant species with high condensed tannin concentration were rejected by ungulates, and were thus considered less palatable.

Plants can respond to herbivore damage (e.g. through grazing or browsing) in two ways (Paige, 1992). Firstly, they can limit herbivore attacks by synthesizing unpalatable chemicals (Ras, 1990; Van der Heyden & Stock, 1999; Hester *et al*., 2006). These unpalatable chemicals such as tannin, also known as plant quantitative defence (Belovsky & Schmitz, 1991), have the ability to decrease herbivore attacks by binding to proteins, thereby becoming indigestible for the herbivore (Harbone, 1991). Other plant compounds such as fibre can also deter herbivore preference (Vallentine, 1990). Therefore, tannin and fibre play a significant role in food selection through their negative correlation with preference (Bergstrom, 1992; Fashing *et al*., 2007). Secondly, instead of synthesizing unpalatable compounds, plants can replace lost tissue by allocating nutrient resources (Richards & Caldwell, 1985; Valentine, 1990; Oesterheld & McNaughton, 1991). This reallocation of nutrient resources makes the plant more tolerant to cope with herbivory (Van der Heyden & Stock, 1995). In addition, maturity also is an important factor that decreases leaf protein content and increases crude fibre and carbohydrate content (Heady, 1964). Animals thus prefer younger shoots and leaves of a plant.

In order to provide guidelines for appropriate grazing management of the remaining fynbos and renosterveld patches, this chapter investigated and compared variations in plant chemical coumpounds (crude fat, crude protein, crude fibre, carbohydrate, mineral content, moisture and tannin). This was specifically aimed at providing greater insight into the forage preference of large indigenous herbivores within three adjacent conservation areas, representing three different grazing intensities over four seasons. This chapter considered the following research questions:

How does herbivory by large game impact on plant palatability across a grazing gradient?
I hypothesized that:

1. Plant compounds will differ between low, medium and high grazing sites. I expect tannin, crude fibre and carbohydrate to be higher on the high grazing site and lower on the low grazing site.
2. Seasonal changes will affect plant compounds, due to differences in plant tissue age.

How does palatability (i.e. plant chemical compounds) influence forage preference of indigenous game under high, medium and low grazing intensities?
I hypothesized that:

1. High protein content, low fibre and low tannin concentration will increase palatability and therefore preference.
2. Protein, fibre and tannin will be the main plant compounds driving forage preference and palatability.

## 3.2 Study area

### 3.2.1 Location

The study was conducted in the low-lying areas (62-150 m a.s.l) of the south-western coastal region of South Africa (Figure 3.1). Study sites were located north of Wellington and east of Hermon in the Tulbagh district of the Western Cape Province (33º23'57.3" S; 19º01'35.8"E to 33º30'43.3"S; 19º03'19.3"E).

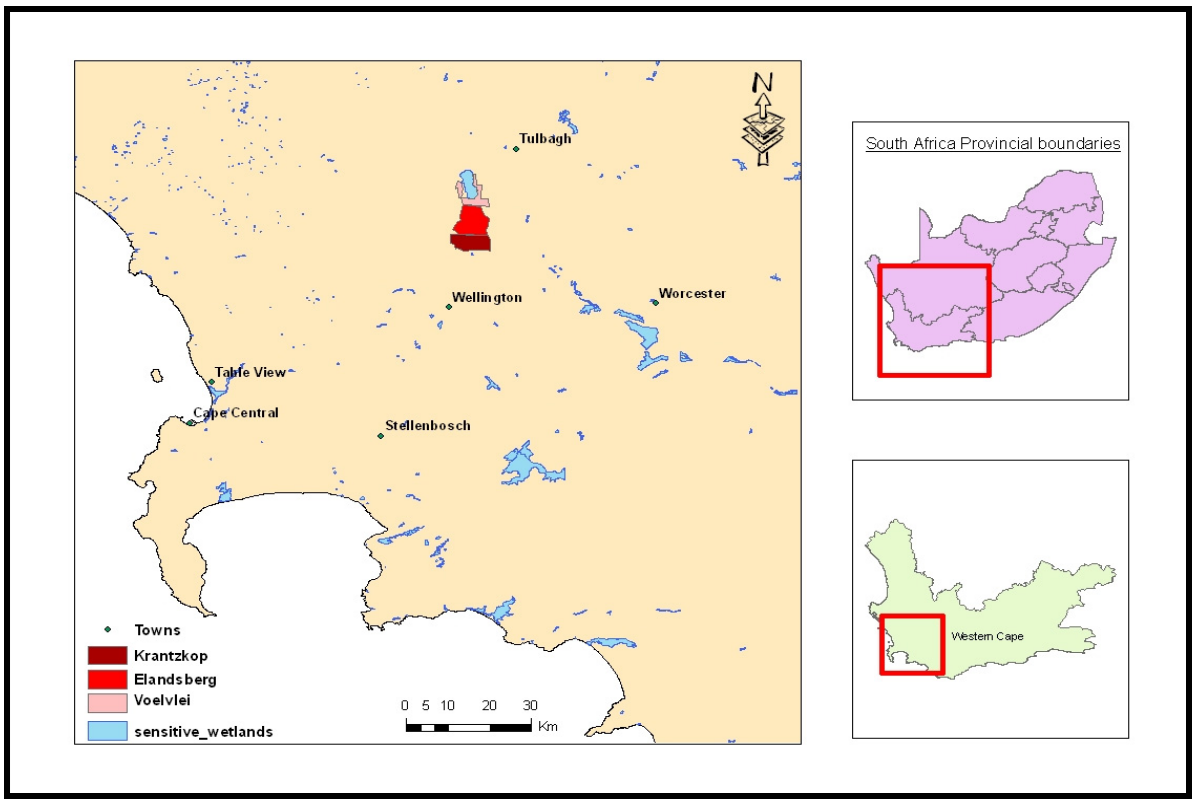


Figure 3.1: Location of the study area indicating the three study sites, Voëlvlei Provincial Nature Reserve (low grazing intensity), Elandsberg Private Nature Reserve (medium grazing intensity), and Krantzkop Ammunition Factory (high grazing intensity).

On the eastern side, the Elandskloof Mountains form a natural boundary to the study area, whereas on the western side it is bordered by privately owned sheep and cereal farms. The study area includes, from the north to the south, Voëlvlei Provincial Nature Reserve (hereafter referred to as Voëlvlei), Elandsberg Private Nature Reserve (hereafter referred to as Elandsberg) and Krantzkop Ammunition Factory (hereafter referred to as Krantzkop). These areas represent three different levels of grazing intensities (Table 3.1).

| Species | Elandsberg 2005 | Krantzkop 2005 | LAU equivalent | Elandsberg (n*LAU) | Krantzkop (n*LAU) |
|---|---|---|---|---|---|
| Black Wildebeest (*Connochaetes* | 82 | 18 | 0.46 | 37.72 | 8.28 |
| Blue Wildebeest (*Connochaetes* | 0 | 30 | 0.50 | 0.00 | 15.00 |
| Bontebok (*Damaliscus dorcas dorcas*) | 155 | 40 | 0.22 | 34.10 | 8.80 |
| Eland (*Taurotragus oryx*) | 114 | 70 | 1.02 | 116.28 | 71.40 |
| Gemsbok (*Oryx gazelle*) | 15 | 50 | 0.56 | 8.40 | 28.00 |
| Red Hartebeest (*Alcephalus* | 25 | 40 | 0.37 | 9.25 | 14.80 |
| Kudu (*Tragelaphus strepsiceros*) | 0 | 5 | 0.42 | 0.00 | 2.10 |
| Mountain Zebra (*Equus zebra*) | 0 | 19 | 0.62 | 0.00 | 11.78 |
| Ostrich (*Struthio camelus australis*) | 19 | 0 | 0.25 | 4.75 | 0.00 |
| Plains Zebra (*Equus burchelli*) | 30 | 5 | 0.66 | 19.80 | 3.30 |
| Springbok (*Antidorcas marsupialis*) | 313 | 450 | 0.15 | 46.95 | 67.50 |
| Grey Rhebok (*Pelea capreolus*) | 0 | 20 | 0.10 | 0.00 | 2.00 |
| Total n | 753 | 765 | | | |
| Total LAU's | | | | 314.97 | 232.96 |
| LAU/ha | | | | 0.09 | 0.12 |

Table 3.1: Stocking rates of large herbivores (surveyed 2005) and Large Animal Units equivalent (LAU) (Van Rooyen, 2002) at Elandsberg (3 000 ha), and Krantzkop (2 000 ha).

*Voëlvlei Provincial Nature Reserve*

Voëlvlei is located to the north of the study area (33º24'11.5"S and 19º02'21.1"E) and covers approximately 2 000 ha. It includes Kasteelskloof and the Voëlvlei Dam water treatment plant managed by CapeNature. Historically, few cattle used to graze in the area before the southern border fence was built in the 1970s (Mike Gregory, personal communication[1]), separating Voëlvlei from Elandsberg. Large game species were never deliberately introduced into this area. However, there are a few small indigenous antelopes such as Steenbok (*Raphicerus campestris*) and Grysbok (*Raphicerus sharpie*) in the reserve. Thus, Voëlvlei was regarded as a control site for the study having low grazing pressure (0 LAU/ha).

[1] Mike Gregor, farm manager, Elandsberg Private Nature Reserve

*Elandsberg Private Nature Reserve*

Elandsberg covers approximately 3 606 ha and is a part of Elandsberg farms. The northern side is bordered by Voëlvlei, on the eastern side by the Elandskloof Mountains.
Abandoned agricultural fields as well as working cereal fields border the western edge. The Krantzkop ammunition factory is located on the southern border. Elandsberg represents the most significant intact remaining fragment of Swartland Alluvium Fynbos / Swartland Shale Renosterveld mosaic (Low & Rebelo, 1996; Nicola Wooding, personal communication[2]). In 1973, Elandsberg was proclaimed a private nature reserve, and will shortly be awarded provincial reserve status (Nicola Wooding, personal communication[2]).

From 1974 to 1982, springbok (*Antidorcas marsupialis*) were introduced to the area. Over the same period, other species such as eland (*Tragephalus oryx*), blue wildebeest (*Connochaetes taurinus*), black wildebeest (*Connochaetes gnou*), red hartebeest (*Alcephalus buselaphus*), gemsbok (*Oryx gazelle*), ostrich (*Struthio camelus australis*), bontebok (*Damaliscus dorcas dorcas*) and mountain zebra (*Equus zebra*) were gradually introduced. However, in 2002, blue wildebeest were removed and sold to other farms (Bernard Wooding, personal communication[3]). In addition, the reserve breeds disease-free African buffalo (*Syncerus caffer caffer*), and takes part in the quagga (*Equus quagga quagga*) breeding programme. In the past, the site used to sustain sheep grazing before the game species were introduced. Furthermore, as a game utilisation and management control, trophy hunting took place, but was stopped in 1996 (Mike Gregor, personal communication[1]). The last game count performed in 2005 gave a value of 0.09 (LAU/ha) (Table 3.1). Elandsberg is an important reserve for the largest population of the endangered geometric tortoise (*Psammobates geometricus*) (Baard, 1990: Baard, 1995).

*Krantzkop Ammunition Factory*

Krantzkop is located in the southern part of the study area, situated at 33º30’28.5” S and 19º02’45.0” E. It was established in December 1978, with a size of approximately 3 000 ha, including the restricted zone (1038.6 ha).

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[1] Mike Gregor, farm manager, Elandsberg Private Nature Reserve

[2]Nicola Wooding, assistant farm manager, Elandsberg Private Nature Reserve

[3]Bernard Wooding, reserve manager, Elandsberg Private Nature Reserve

On the western side of the property is a large area of abandoned old fields. In 1984, the first game species, springbok (*A. marsupialis)* and bontebok (*D. dorcas dorcas*) were introduced (Steve Mitchell, personal communication[4]). Between 1984 and 1986, other species such as grey rhebok (*Pelea capreolus*), plains zebra (*Equus burchelli*), mountain zebra (*Equus zebra*), kudu (*Tragelaphus strepsiceros*), red hartebeest (*Alcephalus buselaphus*), gemsbok (*Oryx gazelle*), eland (*Taurotragus oryx*), blue wildebeest (*Connochaetes taurinus*) and black wildebeest (*Connochaetes gnou*) were gradually introduced.

In 1994, a high number of animals died, either due to internal parasite load, drought or mineral deficiencies (Steve Mitchell, personal communication[4]). Game is counted every year. However, in contrast to Elandsberg, hunting activities are still practiced. In 2005, a large animal unit per hectare (LAU/ha) of 0.12 was recorded, Krantzkop thus represents the highest grazing intensity, compared to Voëlvlei and Elandsberg. Before 1978, no cattle or any domestic livestock were recorded on the property.

### 3.2.2 Climate

The study area falls in the Western Cape coastal lowlands in the winter rainfall region of South Africa. The average mean annual temperature is between 14ºC and 17ºC (Nieman, 1981). Precipitation occurs mainly between May and September (see Figure 3.2). This area is under a strong maritime influence (Rebelo *et al*., 2006), dominated by a mean annual low temperature of 2ºC to 4 ºC. The mean annual precipitation (MAP) is 655 mm with a coefficient of variation of 27 % (Rebelo *et al*., 2006).

[4]Steve Mitchell, reserve manager, Krantzkop

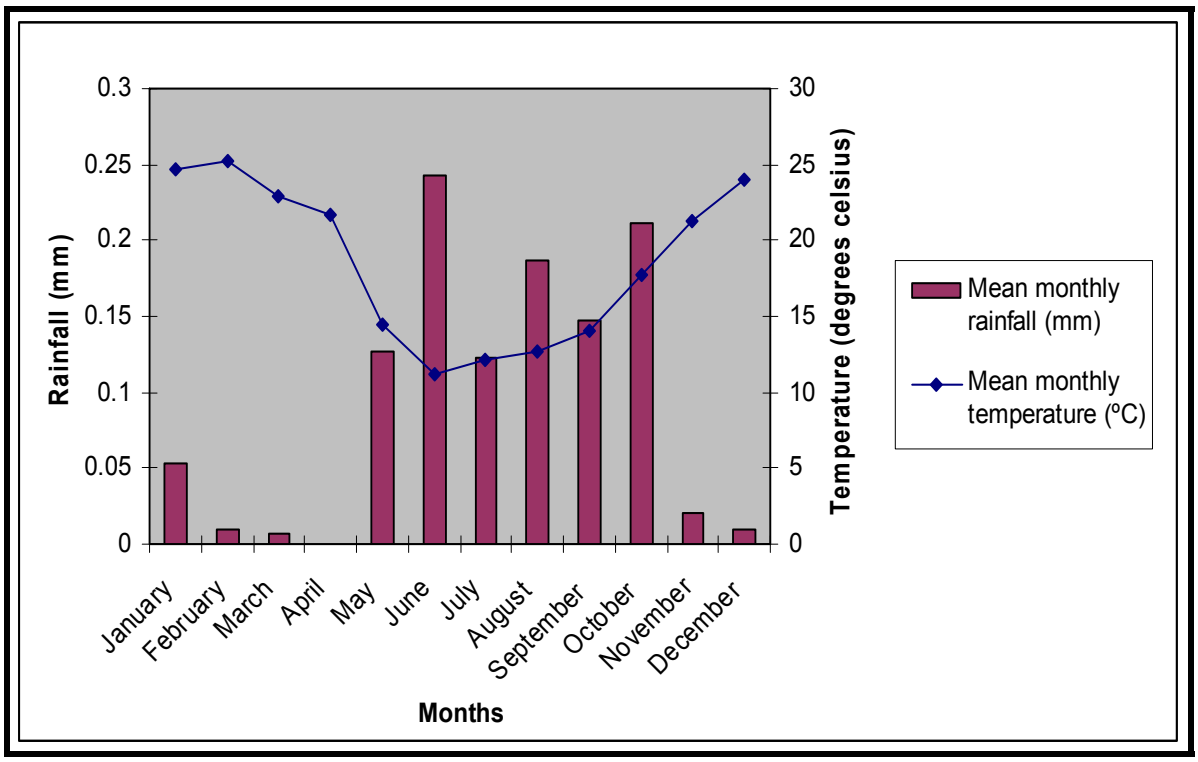


Figure 3.2: Climate diagram of mean monthly temperature and rainfall at Elandsberg Private Nature Reserve (EPNR) in 2005

### 3.2.3 Vegetation

The vegetation type in the study area was formerly classified as West Coast Renosterveld (Baard, 1990; McDowell & Moll, 1992; Low & Rebelo, 1996). However, recently it has been reclassified as Swartland Alluvium Fynbos and Swartland Shale Renosterveld (Rebelo *et al*., 2006). From east to west, Hawequas Sandstone Fynbos is situated at the foothills of the mountains. This leads into an ecotonal zone, where Proteaceae such as *Leucadendron corymbosum* and Restionaceae are well represented. In the west, the natural vegetation is bordered by abandoned old fields of different ages, which serve as a buffer zone to the agricultural fields. Geophytes predominate in the low-lying areas in winter and spring, whereas annual and perennial grasses occupy the open areas year-round.

### 3.2.4 Geology and soil

Soils of the area belong to both the Malmesbury series and Cape granite suite (Merryweather, 1965; Low & Rebelo, 1996; Scheepers & Schoch, 2006). It is composed of duplex, plinthic, silty soils with cobbles and pebbles (Rebelo *et al*., 2006).

## 3.3 Methods

### 3.3.1 Vegetation Surveys

Ten (20x50 m) plots were selected at each site. At Elandsberg, these plots were located on the ten highest ranked hectare plots of the BIOTA (Biodiversity Monitoring Transect Analysis Africa) observatory. Sample plots were oriented north-south, and the geographic coordinates of the southern middle edge were recorded with a handheld GPS. Plots of 20x50m were used to evaluate the presence of species and to collect specimens for identification. Vegetation cover was estimated from percentage canopy cover measured at the 10x10m scale (Figure 3.3). Vegetation surveys were performed seasonally from November 2006 to September 2007 covering four climatic periods.

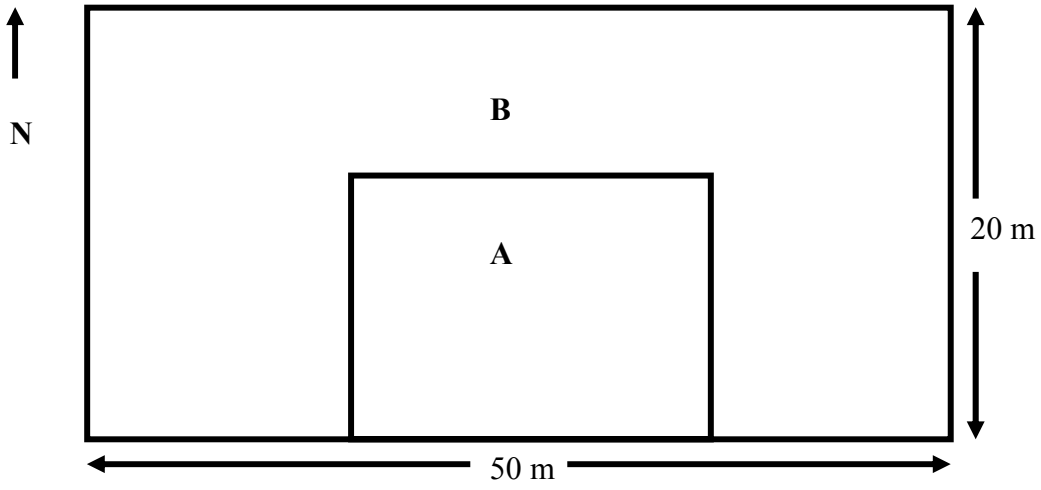


Figure 3.3: Sample plot design to estimate vegetation cover (A=10x10 m; B=20x50 m).

Species were identified using Gibbs-Russell *et al*. (1990), Haaksma and Linder (2000) and Bromilow (2001), or, if unsure, were confirmed by Anne Horn[5] (personal communication), Raphael Kongor[6] (personal communication) and Benjamin Walton (personal communication)

[5]Anne Horn, postdoctoral researcher, Department of Conservation Ecology and Entomology, Stellenbosch University

[6]Raphael Kongor. PhD Student, Department of Conservation Ecology and Entomology, Stellenbosch University.

### 3.3.2 Forage preference evaluation and animal grazing activities

Forage preference was evaluated by modifying the method proposed by Johnson (1980). His method used the difference between the rank of usage by an animal to an item and the rank of availability of this item. The outcome resulting from subtracting rank of usage from rank of availability determines the preference rank of this item to the herbivore. The lower the rank, the higher the preference. In my study, cover of most grasses was less than 1%. This, coupled with the fact that it was difficult to evaluate the percentage cover of species grazed out of the overall species percentage cover, made it not possible to apply this technique directly. Therefore, I ranked the level of grazing for each species and used this as the rank of usage in the study. The scales used to evaluate and rank plant usage after herbivore attacks are reported in Table 3.2. From this point, the preference was evaluated as proposed by Johnson (1980). Animal grazing activities were assessed by the presence of visible signs of browsing or grazing on plants (Figure 3.4).

Table 3.2: Different scales used to evaluate and measure plant damage by herbivores

| life form | Rank usage | observations |
|---|---|---|
| Grass | 3 | not grazed, the plant was undamaged |
| | 2 | moderately grazed, inflorescence and a substantial part of the culms damaged |
| | 1 | heavily grazed, inflorescence, culms and stems damaged down to the ground |
| Shrubs | 4 | not browsed:, the plant was undamaged |
| | 3 | very low level of browsing, only few leaves on a twig damaged |
| | 2 | low browsing, all leaves on a twigs damaged |
| | 1 | moderate browsing, leaves and twigs damaged |
| | 0 | high browsing, whole plant damaged / taken up to the main stem |

Figure 3.4: An example of obvious marks of grazing on *Elegia stipularis* (scored level "2") at Krantzkop in March 2007. Note that almost all stems were removed.

### 3.3.3 Dung collection for germination experiment

Due to their historical presence in the Cape Province during the early European settlement (Skead, 1980), eland (*T. oryx*) and bontebok (*D. dorcas dorcas*) were chosen for the dung collection. Dung pellets were collected as soon as possible after defecation, and stored independently in separate air tight plastic bags for one or two days in the fridge at 10ºC. Germination experiments were conducted between November 2006 and March 2007. In the nursery, the dung pellets were transferred to seedling trays that were filled with sterile sand to avoid seed contamination. Contents of each airtight plastic bag were spread evenly over the sterile sand in one seedling tray. No watering took place until the ambient temperature began to decrease. Trays were watered for one minute per day to activate germination within the dung pellets at the end of March. The watering regime increased to up to five minutes in autumn and winter to mimic the natural environment. The nursery temperature was kept ambient as I wanted the germination process to occur as it would have been in the field. Once seedlings appeared (Figure 3.5), they were removed from the dung pellets and transferred into black propagation bags filled with two thirds compost and one third potting soil. The remaining dung was left on the tray to allow for further germination of seeds.

Figure 3.5: Seed germination trials of bontebok dung in April 2007

### 3.3.4 Plant compound analysis of grazed and non-grazed species

Plants (grazed and non grazed) collected in the field were put in airtight plastic bags and refrigerated at 10ºC for two to five days to avoid water loss through evaporation and biodegradation of the organic matter. Plant samples were oven dried at 50ºC for 72 hours and were ground fine enough to pass through a 0.4 mm sieve. The plant material was kept in tightly closed plastic jars for chemical analysis. Literature commonly cited protein, fibre, tannin and carbohydrate for herbivore preference and plant palatability (Steinke & Booysen, 1968; Georgiadis & McNaughton, 1990; Ras, 1990), however in addition to those, three additional compounds (fat, mineral and moisture) were selected to determine the role they play in affecting preference and palatability and how in turn they could be affected by grazing intensity. Crude fat (weight of material including oils, pigment and fats remaining after immersion into diethyl ether), crude protein (deduction by numerical factor of a residual nitrogen from thermal conductivity cell of the FP-528 determinator), crude fibre (gravimetrical determination of dried residue after digestion of the plant sample with $H_2SO_4$ and NaOH), moisture (mass / weight loss after drying), and mineral content (the proportion of mass that remains after incineration) were assessed following the procedures of Wendt Thiex (2005). The proanthocyanidin method following Hagerman (1995) was used for condensed

tannin. No calibration using quebracho was done, therefore only the relative values were used for comparison data analysis. Carbohydrate (as nitrogen-free extractives) was determined following McDonald *et al*., (2002). All results were expressed on plant dry material basis, excepted moisture, which was expressed as percentage wet plant material *per se*.

### 3.3.5 Statistical analyses

Since some of the species were not represented in all sites, only *Tribolium unioleae, Hyparrhenia hirta* (Poaceae)*, Montinia caryophyllacea* (Montiniaceae)*, Ischyrolepis capensis* (Restionaceae)*,* and *Ficinia sp.* (Cyperaceae) were chosen to determine the chemical attributes that grazed plants display under different grazing intensities in each season. Additionally, the ungrazed *Elytropappus rhinocerotis* (Asteraceae) was chosen to test for environmental variation across the study area (i.e. variation not related directly to grazing). Plant compounds were compared across the grazing gradient using a one-way ANOVA and Post Hoc Bonferroni comparisons in STATISTICA (STATISTICA 8, Statsoft, Inc. 2007). Kruskal-Wallis ANOVA was used when the assumption of homogeneity of variance (Levene's test and Brown-Forsythe's test) and normality of residuals (Shapiro-Wilk test) were rejected. When plant material was only available for two sites, a *t*-test was performed to compare the values of the same plant compound in the same season. The Mann-Whitney U test was used when the assumption of homogeneity of variance was rejected (Levene's test).

Furthermore, to understand how plant chemical compounds affect preference and palatability in high and medium grazing intensity in each season, twenty species were selected (Appendix A). This selection included grazed and non-grazed plants. To assess the relationship of those various plant chemical compounds with grazing preference and palatability, a Principal Component Analysis (PCA) was performed.

## 3.4 Results

### 3.4.1 Vegetation survey

In total, one hundred and ninety five species were recorded for the study area over a year (Appendix B). At Voëlvlei and Krantzkop, *E. rhinocerotis* (Asteraceae) was the most dominant species. At Elandsberg, Restionaceae and Proteaceae were dominant. Throughout the year, different species of the Poaceae family occurred in the natural vegetation (Table 3.2). Additionally, some alien grass species (such as *Briza maxima, Vulpia myuros*) were also recorded.

### 3.4.2 Forage preference evaluation and animal grazing activities

Sixteen plants species were found with obvious grazing marks. Species grazed were mainly grass, restios and sedges (Table 3.3 and Table 3.4), but grasses were most grazed overall. In each season, different species of grass and sedges occurred and were grazed in a different way. For instance, *F. indica* in spring and summer was completely grazed at the high and medium grazing intensity site (rank preference "1"), while *T. unioleae* in spring was not grazed at the high grazing intensity site (rank preference "4"), but partially grazed in summer (rank preference "2"). In general, species such as *F. indica, Eragrostis sp., Lolium sp., H. hirta, V. myorus* and *S. barbata* were highly preferred and represented less than 1% of the vegetation cover. Both the medium and the high grazing site showed the same trends in percentage vegetation cover. In addition, a pattern emerged showing that the grazing intensity was less than it had been in the previous season for a given species. For instance, as seasons changed, species such as *T. unioleae* showed a decrease in "rank preference" from summer to autumn (Table 3.4).

Table 3.3: Percentage cover and preference rank of ten most grazed (1-2 = highly preferred; 3 = moderately preferred; 4-5 = avoided) species across seasons (spring, summer, autumn and winter) at Elandsberg.

| Medium intensity grazing (Elandsberg) | | | | |
|---|---|---|---|---|
| Season | Family | Botanical name | % cover | Ranked preference |
| Spring | Montiniaceae | *Montinia caryophyllacea* | 5 | 3 |
| | Cyperaceae | *Ficinia indica* | <1 | 1 |
| | Poaceae | *Lolium sp.** | <1 | 1 |
| | Poaceae | *Vulpia myuros** | <1 | 1 |
| | Poaceae | *Themeda triandra* | <1 | 3 |
| | Poaceae | *Ehrharta sp.* | <1 | 4 |
| | Restionaceae | *Ischyrolepis capensis* | 2 | 2 |
| | Restionaceae | *Ischyrolepis sp3.* | 2 | 2 |
| Summer | Asteraceae | *Elytropappus rhinocerotis* | 1 | 4 |
| | Poaceae | *Themeda triandra* | <1 | 2 |
| | Poaceae | *Grass 4* | <1 | 3 |
| | Restionaceae | *Ischyrolepis capensis* | 2 | 1 |
| | Restionaceae | *Elegia stipularis* | 2 | 2 |
| | Restionaceae | *Ischyrolepis sp2.* | 2 | 3 |
| Autumn | Asteraceae | *Elytropappus rhinocerotis* | 1 | 5 |
| | Montiniaceae | *Montinia caryophyllacea* | 2 | 2 |
| | Cyperaceae | *Ficinia sp.* | <1 | 3 |
| | Poaceae | *Cynodon dactylon* | <1 | 1 |
| | Poaceae | *Hyparrhenia hirta* | <1 | 1 |
| | Poaceae | *Eragrostis sp.* | <1 | 2 |
| | Poaceae | *Grass 4* | <1 | 4 |
| | Poaceae | *Tribolium unioleae* | <1 | 4 |
| | Restionaceae | *Elegia stipularis* | <1 | 4 |
| | Restionaceae | *Ischyrolepis capensis* | <1 | 4 |
| | Restionaceae | *Ischyrolepis sp3.* | <1 | 4 |
| Winter | Asteraceae | *Elytropappus rhinocerotis* | 2 | 4 |
| | Montiniaceae | *Montinia caryophyllaceae* | 2 | 2 |
| | Cyperaceae | *Ficinia sp.* | <1 | 2 |
| | Poaceae | *Hyparrhenia hirta* | <1 | 1 |
| | Poaceae | *Ehrharta sp.* | <1 | 3 |
| | Restionaceae | *Ischyrolepis capensis* | <1 | 3 |
| | Restionaceae | *Elegia stipularis* | <1 | 5 |

Ranked preference was determined following Johnson (1980); * Alien species

Table 3.4: Percentage cover and preference rank of ten most grazed (1-2 = highly preferred; 3 = moderately preferred; 4-5 = avoided) species across seasons (spring, summer, autumn and winter) at Krantzkop.

| High intensity grazing (Krantzkop) | | | | |
|---|---|---|---|---|
| Season | Family | Botanical name | % cover | Ranked preference |
| Spring | Caryophyllaceae | *Montinia sp.* | 10 | 3 |
| | Cyperaceae | *Ficinia indica* | <1 | 1 |
| | Poaceae | *Eragrostis sp.* | <1 | 1 |
| | Poaceae | *Lolium sp.** | <1 | 1 |
| | Poaceae | *Schismus barbatus* | <1 | 1 |
| | Poaceae | *Vulpia myuros** | <1 | 1 |
| | Poaceae | *Ehrharta sp.* | <1 | 4 |
| | Poaceae | *Tribolium unioleae* | <1 | 4 |
| | Restionaceae | *Elegia stipularis* | <1 | 1 |
| | Restionaceae | *Ischyrolepis capensis* | 2 | 2 |
| Summer | Asteraceae | *Elytropappus rhinocerotis* | 25 | 5 |
| | Caryophyllacea | *Montinia sp.* | 10 | 2 |
| | Cyperaceae | *Ficinia indica* | <1 | 1 |
| | Poaceae | *Hyparrhenia hirta* | <1 | 1 |
| | Poaceae | *Eragrostis sp.* | <1 | 2 |
| | Poaceae | *Tribolium unioleae* | <1 | 2 |
| | Poaceae | *Grass 4* | <1 | 4 |
| | Restionaceae | *Ischyrolepis capensis* | 2 | 1 |
| | Restionaceae | *Elegia stipularis* | <1 | 3 |
| Autumn | Asteraceae | *Elytropappus rhinocerotis* | <1 | 5 |
| | Caryophyllacea | *Montinia sp.* | 10 | 2 |
| | Cyperaceae | *Ficinia sp.* | <1 | 3 |
| | Poaceae | *Cynodon dactylon* | <1 | 1 |
| | Poaceae | *Hyparrhenia hirta* | <1 | 1 |
| | Poaceae | *Eragrostis sp.* | <1 | 2 |
| | Poaceae | *Grass 3* | <1 | 4 |
| | Poaceae | *Tribolium unioleae* | <1 | 4 |
| | Restionaceae | *Elegia stipularis* | <1 | 4 |
| | Restionaceae | *Ischyrolepis capensis* | <1 | 4 |
| Winter | Asteraceae | *Elytropappus rhinocerotis* | 25 | 5 |
| | Caryophyllacea | *Montinia sp.* | 10 | 2 |
| | Cyperaceae | *Ficinia sp.* | <1 | 2 |
| | Poaceae | *Cynodon dactylon* | <1 | 1 |
| | Poaceae | *Hyparrhenia hirta* | <1 | 1 |
| | Poaceae | *Ehrharta sp.* | <1 | 3 |
| | Poaceae | *Briza maxima** | <1 | 4 |
| | Restionaceae | *Ischyrolepis capensis* | <1 | 3 |

Ranked preference was determined following Johnson (1980); * Alien species

### 3.4.3 Dung collection for germination trial

After five months of observation in the nursery, seedlings started to emerge in March when the average temperature began to decrease. Species from different families and genera germinated but grasses were the most dominant. Grasses represented over 85% of seedlings emerging from both eland and bontebok dung (Table 3.5), with alien grasses representing

58% of seedlings in eland dung, and 60% of seedlings in bontebok dung. Three alien species (*L. perenne, V. myuros* and *B. maxima*) were found most often in the dung of the two species.

Table 3.5: Relative frequency of seedlings germinated from 63 eland dung pellets and 72 bontebok dung pellets

| Botanical name | Family | Relative frequency (%) | |
|---|---|---|---|
| | | eland | bontebok |
| *Briza maxima** | *Poaceae* | 1.59 | 9.72 |
| *Briza minor** | *Poaceae* | 1.59 | 1.39 |
| *Cynodon dactylon* | *Poaceae* | 4.76 | 6.94 |
| *Eragrostis sp.* | *Poaceae* | 4.76 | 4.17 |
| *Ficinia sp.* | *Cyperaceae* | 4.76 | 2.78 |
| *Forb 1* | *Unknown* | 1.59 | 1.39 |
| *Forb 2* | *Unknown* | 1.59 | 2.78 |
| *Grass 3* | *Poaceae* | 1.59 | 1.39 |
| *Lepidium sp.* | *Poaceae* | 1.59 | 0.00 |
| *Lolium sp.** | *Poaceae* | 26.98 | 5.56 |
| *Plantago sp.* | *Poaceae* | 1.59 | 0.00 |
| *Poa annua** | *Poaceae* | 3.17 | 2.78 |
| *Romulea sp.* | *Iridaceae* | 1.59 | 0.00 |
| *Stellaria sp.* | *Caryophyllaceae* | 1.59 | 0.00 |
| *Tribolium hispidum* | *Poaceae* | 1.59 | 4.17 |
| *Unknown* | *Poaceae* | 7.94 | 0.00 |
| *Vulpia myuros** | *Poaceae* | 15.87 | 22.22 |
| Family frequency in dung | Poaceae | 88 | 92 |
| | Cyperaceae | 4 | 4 |
| | Unknown | 8 | 4 |
| Alien | Poaceae | 58 | 60 |
| Indigenous | Poaceae | 42 | 40 |

* Alien species

### 3.4.4 Impacts of grazing on plant chemical compounds

The analyses of crude fat, crude protein, crude fibre, mineral carbohydrate and moisture revealed some interesting patterns. The results for the species chosen for testing environmental parameters (*E. rhinocerotis*) across the study area showed that there were no significant differences in chemical compounds between different grazing intensities (Table 3.6). However, there were seasonal differences observed in plant compounds, e.g. between winter and summer for crude protein (d.f. = 7, t = -3.655, P = 0.008, Table 3.7), plant moisture (d.f. = 7, t = -5.385, P = 0.001) on the high grazing site (Table 3.7) and crude fibre (d.f. = 9, t = -2.573, P = 0.030) on the low grazing intensity site.

The results of the grazed species, *I. capensis* (Table 3.8), *H. hirta* (Table 3.9), *M. caryophyllacea* (Table 3.10), *T. unioleae* (Table 3.11) and *Ficinia sp.* (Table 3.12), are presented by compounds. This allows for a better understanding of the effect of grazing intensity on those compounds.

*Crude fat*

Of the five species analysed, only two showed significant differences between the three different grazing intensities. In autumn, for *M. caryophyllacea*, crude fat content was significantly higher at the low grazing site than at the high grazing site ($F_{2.11} = 6.748$, $P = 0.012$, Table 3.10), while for *T. unioleae*, crude fat content was significantly higher on the high grazing site than on the low grazing site ($F_{2,17} = 5.425$, $P = 0.015$, Table 3.11).

*Crude protein*

In the crude protein analysis, three species showed significant differences (Table 3.8; Table 3.10 and 3.12). The crude protein level for *I. capensis* was significantly higher at the high grazing site than at the low grazing site in winter ($F_{2, 10} = 4.341$, $P = 0.043$, Table 3.8). For *M. caryophyllacea*, the level of the crude protein was significantly higher at the low grazing site than at the higher grazing site in summer ($H_{1.7} = 4.5$, $P = 0.034$, Table 3.10). Although the results were not significant during other seasons, there was a trend showing that the level of crude protein was higher at the high grazing site than at the low grazing site in winter. However, as seasons changed, this trend tended to progress in the opposite direction. As a result, crude protein level was higher at both medium and low grazing sites than at the high grazing site in autumn. For *Ficinia sp.*, the level of the crude protein was significantly higher at the higher grazing site than at the medium grazing site in winter ($F_{2, 15} = 4.868$, $P = 0.02$, Table 3.12).

*Crude fibre*

The comparisons of crude fibre showed that *T. unioleae* (Table 3.11) was the only species showing significant differences between sites. The crude fibre content was significantly higher at the low grazing site than at the high grazing site in summer (d.f. = 12, $t = - 4.044$, $P = 0.001$). Even though there were no significant differences for other seasons, there was still a trend showing that as seasons changed from spring to autumn, the crude fibre level at the high grazing site decreased.

*Mineral (total ash)*

The value of mineral for *T. unioleae* was significantly lower at the high grazing site than at the low grazing site in summer (d.f. = 12, t = -3.988, P = 0.001). Apart from this, the compound showed no other trends for any of the other species in all seasons.

*Carbohydrate*

Three species showed significant differences in carbohydrate content. The value of carbohydrate of *I. capensis* is significantly lower at the high grazing site than at medium grazing site in summer ($F_{2, 0} = 5.86$, P = 0.009). For *Ficinia sp.*, carbohydrate values were significantly lower at the high grazing site than at the low grazing site in winter ($F_{2, 15} = 9.126$, P = 0.002). The carbohydrate value of *T. unioleae* was significantly higher at the low grazing site than at the high grazing site in summer (d.f. = 12, t = 4.541, P = 0.001). Although the carbohydrate value for *T. unioleae* was only significantly different in summer, the general trend showed that it tended to be higher at the high grazing site in each season. A similar pattern was observed for *H. hirta*.

*Moisture*

Overall, four species were found with significant differences in moisture content. For *I. capensis*, moisture content was significantly higher at the high grazing site than at the low grazing site in summer ($F_{2, 20} = 4.9297$, P = 0.019), for *M. caryophyllacea* in autumn ($F_{2.11} = 6.78$, P = 0.1206). However, moisture levels of *Ficinia sp.* were significantly higher at the high grazing site than at the medium grazing site ($F_{2, 15} = 5.812$, P = 0.013) in autumn.

*Tannin*

*M. caryophyllacea* was the only species in which tannin concentration was significantly higher at the high grazing site than the medium grazing site in winter (d.f. = 6, t = 3.086, P = 0.021). However, although no significant differences were observed within other seasons, the trend showed that the value of tannin was the highest on the high grazing site. A similar pattern was observed for *Ficinia sp.*

Table 3.6: Comparison of *Elytropappus rhinocerotis* chemical compounds (means ± s.d) between different grazing sites in winter and summer. Sites in winter and summer showed non-significant differences (p> 0.05).

| | Winter | | | Summer | | |
|---|---|---|---|---|---|---|
| Nutrient | High | Medium | Low | High | Medium | Low |
| Crude fat (%) | 12.16 ± 1.90 | 12.23 ± 1.27 | 14.10 ± 0.69 | 13.33 ± 3.14 | 16.16 ± 2.61 | 15.38 ± 2.77 |
| Crude protein (%) | 7.48 ± 0.72 | 6.30 ± 0.80 | 5.94 ± 1.27 | 5.44 ± 0.82 | 6.58 ± 0.19 | 6.86 ± 2.12 |
| Crude fibre (%) | 32.09 ± 5.63 | 31.19 ± 5.32 | 31.85 ± 3.44 | 28.65 ± 3.37 | 32.04 ± 0.35 | 27.89 ± 1.81 |
| Mineral (%) | 3.75 ± 0.18 | 4.40 ± 0.33 | 3.82 ± 0.04 | 4.01 ± 0.45 | 3.94 ± 0.32 | 4.02 ± 0.17 |
| Carbohydrate (%) | 44.52 ± 6.78 | 45.88 ± 6.12 | 44.28 ± 2.24 | 48.57 ± 3.65 | 41.28 ± 2.13 | 45.85 ± 3.23 |
| Moisture (%) | 46.47 ± 1.30 | 40.73 ± 1.64 | 46.54 ± 4.12 | 38.94 ± 2.19 | 36.76 ± 4.43 | 37.12 ± 1.53 |
| Tannin (mg/ml) | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| | n = 3 | n = 2 | n = 3 | n = 6 | n = 2 | n = 8 |

Table 3.7: Comparison of *Elytropappus rhinocerotis* chemical compounds (means ± s.d) to test the effect of environmental parameters across the study area between summer and winter. Letters indicate significant differences at 95 % confidence intervals.

| | Winter | | | Summer | | |
|---|---|---|---|---|---|---|
| Nutrient | High | Medium | Low | High | Medium | Low |
| Crude fat (%) | 12.16 ± 1.90 | 12.23 ± 1.27 | 14.10 ± 0.69 | 13.33 ± 3.14 | 16.16 ± 2.61 | 15.38 ± 2.77 |
| Crude protein (%) | $7.48^{b}$ ± 0.72 | 6.30 ± 0.80 | 5.94 ± 1.27 | $5.44^{a}$ ± 0.82 | 6.58 ± 0.19 | 6.86 ± 2.12 |
| Crude fibre (%) | 32.09 ± 5.63 | 31.19 ± 5.32 | $31.85^{b}$ ± 3.44 | 28.65 ± 3.37 | 32.04 ± 0.35 | $27.9^{a}$ ± 1.81 |
| Mineral (%) | 3.75 ± 0.18 | 4.40 ± 0.33 | 3.82 ± 0.04 | 4.01 ± 0.45 | 3.94 ± 0.32 | 4.02 ± 0.17 |
| Carbohydrate (%) | 44.52 ± 6.78 | 45.88 ± 6.12 | 44.28 ± 2.24 | 48.57 ± 3.65 | 41.28 ± 2.13 | 45.85 ± 3.23 |
| Moisture (%) | $46.47^{b}$ ± 1.30 | 40.73 ± 1.64 | 46.54 ± 4.12 | $38.94^{a}$ ± 2.19 | 36.76 ± 4.43 | 37.12 ± 1.53 |
| Tannin (mg/ml) | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| | n = 3 | n = 2 | n = 3 | n = 6 | n = 2 | n = 8 |

Table 3.8: Ranked preference variation (1-5) and comparisons of *Ischyrolepis capensis* chemical compounds across a grazing intensity over four seasons (means ± s.d). Letters indicate significant differences at 95 % confidence intervals. Empty columns denote the lack of sampling material at the specific site.

| | Winter | | | Spring | | | Summer | | | Autumn | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ranked preference | 4 | | | 2 | | | 1 | | | 4 | | |
| Nutrient | High | Medium | Low | High | Medium | Low | High | Medium | Low | High | Medium | Low |
| Crude fat (%) | 4.68 ± 4.18 | 2.18 ± 3.01 | 1.00 ± 0.20 | 2.74 ± 2.94 | 1.00 ± 0.59 | - | 3.17 ± 3.45 | 1.00 ± 0.13 | 0.98 ± 0.17 | 1.62 ± 2.18 | 0.97 ± 0.07 | 3.16 ± 3.53 |
| Crude protein (%) | 24.5$^{a}$ ± 12.9 | 9.29$^{ab}$ ± 9.81 | 3.99$^{bc}$ ± 1.29 | 7.33 ± 1.86 | 6.27 ± 1.29 | - | 5.59 ± 1.17 | 4.99 ± 0.41 | 5.49 ± 0.78 | 5.73 ± 2.27 | 6.08 ± 0.71 | 6.15 ± 0.60 |
| Crude fibre (%) | 30.25 ± 6.43 | 34.39 ± 6.01 | 36.78 ± 1.29 | 29.75 ± 9.07 | 31.31 ± 4.39 | - | 37.42 ± 7.14 | 32.7 ± 2.09 | 32.48 ± 2.54 | 40.34 ± 9.40 | 43.85 ± 9.66 | 43.01 ± 8.51 |
| Mineral (%) | 4.70 ± 2.01 | 3.11 ± 2.52 | 2.43 ± 0.44 | 4.74 ± 2.03 | 3.69 ± 1.66 | - | 3.44 ± 1.78 | 2.03 ± 0.34 | 2.11 ± 0.18 | 2.61 ± 0.78 | 2.22 ± 0.23 | 2.25 ± 0.25 |
| Carbohydrate (%) | 35.83 ± 18.99 | 51.0 ± 13.25 | 55.78 ± 0.99 | 55.42 ± 10.45 | 68.15 ± 21.05 | - | 50.36$^{a}$ ± 8.77 | 59.61$^{b}$ ± 2.43 | 58.9$^{cb}$ ± 2.61 | 49.68 ± 11.02 | 46.86 ± 9.30 | 45.41 ± 12.32 |
| Moisture (%) | 56.76 ± 13.75 | 45.69 ± 11.69 | 32.61 ± 9.36 | 49.53 ± 12.40 | 50.47 ± 11.66 | - | 44.15$^{a}$ ± 22.75 | 25.5$^{ab}$ ± 3.72 | 22.53$^{b}$ ± 2.36 | 42.43 ± 13.04 | 31.05 ± 4.12 | 37.02 ± 4.86 |
| Tannin (mg/ml) | 0.27 ± 0.55 | 1.35 ± 44 | 3.93 ± 2.61 | 8.84 ± 12.71 | 12.76 ± 18.94 | - | 1.76 ± 3.51 | 5.18 ± 8.42 | 3.29 ± 6.63 | 5.43 ± 7.11 | 0.52 ± 0.98 | 3.00 ± 3.72 |
| | n = 10 | n = 6 | n = 7 | n = 6 | n = 3 | n = 0 | n = 10 | n = 6 | n = 7 | n = 10 | n = 5 | n = 3 |

Table 3.9: Ranked preference variation (1-5) and comparisons of *Hyparrhenia hirta* chemical compounds across a grazing intensity over four seasons (means ± s.d). Letters indicate significant differences at 95 % confidence intervals. Empty columns denote the lack of sampling material at the specific site.

| | Winter | | | Spring | | | Summer | | | Autumn | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ranked preference | 1 | | | | | | | | | 1 | | |
| Nutrient | High | Medium | Low | High | Medium | Low | High | Medium | Low | High | Medium | Low |
| Crude fat (%) | 1.25 ± 0.24 | 1.27 ± 0.43 | 1.36 ± 0.33 | - | - | - | - | - | - | 1.80 ± 0.64 | 1.71 ± 0.22 | 1.61 ± 0.14 |
| Crude protein (%) | 25.07 ± 15.14 | 17.27 ± 3.40 | 24.26 ± 7.21 | - | - | - | - | - | - | 6.58 ± 1.64 | 4.93 ± 2.74 | 7.11 ± 0.68 |
| Crude fibre (%) | 33.37 ± 0.17 | 44.16 ± 8.04 | 40.89 ± 6.65 | - | - | - | - | - | - | 38.30 ± 8.00 | 41.44 ± 1.10 | 42.11 ± 4.78 |
| Mineral (%) | 4.48 ± 1.61 | 4.03 ± 0.16 | 4.92 ± 0.78 | - | - | - | - | - | - | 7.19 ± 1.33 | 5.31 ± 1.05 | 6.32 ± 0.28 |
| Carbohydrate (%) | 35.82 ± 13.46 | 33.16 ± 4.37 | 28.57 ± 13.31 | - | - | - | - | - | - | 46.12 ± 7.45 | 46.6 ± 0.37 | 42.86 ± 3.70 |
| Moisture (%) | 67.3 ± 0.01 | 57.39 ± 4.07 | 63.08 ± 4.62 | - | - | - | - | - | - | 58.90 ± 11.68 | 50.07 ± 50.07 | 57.36 ± 57.36 |
| Tannin (mg/ml) | 0.11 ± 0.15 | 1.15 ± 0.78 | 0.57 ± 0.37 | - | - | - | - | - | - | 1.43 ± 2.47 | 0 | 0 |
| | n = 2 | n = 2 | n = 4 | n = 0 | n = 0 | n = 0 | n = 0 | n = 0 | n = 0 | n = 3 | n = 2 | n = 2 |

Table 3.10: Ranked preference (1-5) and comparisons of *Montinia caryophyllacea* chemical compounds across a grazing intensity over four seasons (means ± s.d). Letters indicate significant differences at 95 % confidence intervals. Empty columns denote the lack of sampling material at the specific site.

| | Winter | | | Spring | | | Summer | | | Autumn | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ranked preference | 3 | | | 3 | | | 2 | | | 2 | | |
| Nutrient | High | Medium | Low | High | Medium | Low | High | Medium | Low | High | Medium | Low |
| Crude fat (%) | 1.82 ± 0.41 | 2.29 ± 0.15 | - | 1.82 ± 0.80 | 2.04 ± 0.14 | 2.17 ± 0.22 | 2.61 ± 01.67 | - | 2.25 ± 0.35 | $2.3^{a}$ ± 0.27 | $2.33^{ab}$ ± 0.16 | $2.88^{b}$ ± 0.30 |
| Crude protein (%) | 19.26 ± 7.91 | 21.14 ± 11.1 | - | 6.95 ± 1.20 | 5.55 ± 1.19 | 4.64 ± 0.23 | $4.63^{a}$ ± 0.55 | - | $9.22^{b}$ ± 4.04 | 6.82 ± 1.77 | 10.44 ± 8.34 | 10.14 ± 2.24 |
| Crude fibre (%) | 27.25 ± 10.81 | 38.34 ± 1.63 | - | 21.99 ± 8.71 | 20.16 ± 1.84 | 20.95 ± 0.97 | 30.04 ± 8.42 | - | 23.63 ± 5.56 | 30.78 ± 8.81 | 32.96 ± 6.10 | 24.29 ± 4.64 |
| Mineral (%) | 6.28 ± 1.81 | 3.20 ± 0.34 | - | 5.16 ± 0.53 | 4.44 ± 0.90 | 4.22 ± 0.79 | 4.58 ± 1.02 | - | 3.50 ± 0.48 | 4.51 ± 1.14 | 4.90 ± 0.73 | 4.17 ± 1.09 |
| Carbohydrate (%) | 45.4 ± 10.86 | 35.01 ± 9.25 | - | 64.05 ± 9.09 | 67.79 ± 1.29 | 67.99 ± 1.31 | 58.12 ± 10.00 | - | 61.32 ± 9.61 | 55.58 ± 8.08 | 49.36 ± 13.6 | 58.5 ± 5.23 |
| Moisture (%) | 57.7 ± 20.32 | 64.57 ± 1.44 | - | 59.13 ± 6.61 | 58.66 ± 1.42 | 52.46 ± 7.56 | 45.78 ± 2.27 | - | 48.17 ± 8.37 | $64.02^{a}$ ± 4.24 | $62.25^{ab}$ ± 0.83 | $71.57^{b}$ ± 3.97 |
| Tannin (mg/ml) | $14.3^{a}$ ± 5.21 | $2.02^{b}$ ± 2.37 | - | 13.98 ± 6.97 | 7.99 ± 3.06 | 3.10 ± 0.98 | 12.28 ± 8.50 | - | 4.61 ± 3.18 | 9.67 ± 7.44 | 2.85 ± 0.89 | 5.89 ± 0.28 |
| | n = 6 | n = 2 | n = 0 | n = 7 | n = 4 | n = 2 | n = 3 | n = 0 | n = 4 | n = 7 | n = 3 | n = 4 |

Table 3.11: Ranked preference (1-5) and comparisons of *Tribolium unioleae* chemical compounds across a grazing intensity over four seasons (means ± s.d). Letters indicate significant differences at 95 % confidence intervals. Empty columns denote the lack of sampling material at the specific.

| | Winter | | | Spring | | | Summer | | | Autumn | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ranked preference | | | | 4 | | | 2 | | | 4 | | |
| Nutrient | High | Medium | Low | High | Medium | Low | High | Medium | Low | High | Medium | Low |
| Crude fat (%) | - | - | - | 1.31 ± 0.14 | 1.30 ± 0.18 | 1.42 ± 0.25 | 1.41 ± 0.14 | - | 1.36 ± 0.05 | $1.70^{a}$ ± 0.14 | $1.38^{b}$ ± 0.12 | $1.40^{bc}$ ± 0.29 |
| Crude protein (%) | - | - | - | 6.36 ± 0.16 | 6.98 ± 0.52 | 6.76 ± 0.46 | 5.77 ± 0.39 | - | 5.76 ± 0.67 | 11.54 ± 6.27 | 7.26 ± 2.16 | 7.05 ± 1.19 |
| Crude fibre (%) | - | - | - | 35.56 ± 4.22 | 35.48 ± 1.73 | 35.46 ± 2.05 | $32.81^{a}$ ± 2.04 | - | $37.85^{b}$ ± 2.57 | 36.53 ± 6.49 | 53.15 ± 11.22 | 40.40 ± 14.40 |
| Mineral (%) | - | - | - | 4.33 ± 0.42 | 4.67 ± 0.13 | 5.12 ± 1.00 | $3.96^{a}$ ± 0.50 | - | $5.04^{b}$ ± 0.45 | 7.20 ± 7.24 | 6.03 ± 6.04 | 6.79 ± 6.80 |
| Carbohydrate (%) | - | - | - | $52.42^{a}$ ± 4.07 | $51.57^{b}$ ± 1.81 | $51.24^{ab}$ ± 1.53 | $56.05^{a}$ ± 2.28 | - | $49.98^{b}$ ± 2.60 | 42.99 ± 8.21 | 32.16 ± 11.46 | 44.35 ± 14.32 |
| Moisture (%) | - | - | - | 48.26 ± 2.80 | 42.66 ± 4.43 | 40.1 ± 4.7 | 25.82 ± 4.19 | - | 24.43 ± 1.90 | 51.35 ± 2.97 | 49.82 ± 2.04 | 49.98 ± 5.66 |
| Tannin (mg/ml) | - | - | - | 0.00 | 0.00 | 0.08 ± 0.20 | 3.99 ± 11.94 | - | 0.00 | 0.00 | 0.00 | 0.00 |
| | n = 0 | n = 0 | n = 0 | n = 5 | n = 5 | n = 6 | n = 9 | n = 0 | n = 5 | n = 9 | n = 4 | n = 7 |

Table 3.12: Ranked preference (1-5) and comparisons of *Ficinia sp.* chemical compounds across a grazing intensity over four seasons (means ± s.d). Letters indicate significant differences at 95 % confidence intervals. Empty columns denote the lack of sampling material at the specific site.

| | Winter | | | Spring | | | Summer | | | Autumn | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Ranked preference | 1 | | | | | | | | | 1 | | |
| Nutrient | High | Medium | Low | High | Medium | Low | High | Medium | Low | High | Medium | Low |
| Crude fat (%) | 2.69 ± 0.63 | 2.52 ± 0.61 | 3.22 ± 0.39 | - | - | - | - | - | - | 2.60 ± 0.63 | 2.53 ± 0.61 | 3 .22 ± 0.39 |
| Crude protein | $25.10^{a}$ ± 5.14 | $16.29^{b}$ ± 5.63 | $21.3^{ab}$ ± 4.73 | - | - | - | - | - | - | 25.10 ± 5.13 | 16.29 ± 5.62 | 21.30 ± 4.72 |
| Crude fibre (%) | 34.55 ± 6.49 | 29.77 ± 5.35 | 26.80 ± 3.66 | - | - | - | - | - | - | 34.56 ± 6.48 | 29.77 ± 5.35 | 26.80 ± 3.66 |
| Mineral (%) | 6.09 ± 0.60 | 5.04 ± 0.82 | 6.09 ± 0.95 | - | - | - | - | - | - | 6.09 ± 0.6 | 5.04 ± 0.82 | 6.09 ± 0.95 |
| Carbohydrate | $31.55^{a}$ ± 3.73 | $46.36^{b}$ ± 10.5 | $42.7^{bc}$ ± 2.81 | - | - | - | - | - | - | 31.55 ± 3.70 | 46.36 ± 10.5 | 42.57 ± 2.81 |
| Moisture (%) | 62.51 ± 10.5 | 57.93 ± 6.23 | 59.87 ± 4.76 | - | - | - | - | - | - | $62.51^{a}$ ± 10.53 | $57.9^{b}$ ± 6.23 | $59.9^{bc}$ ± 4.76 |
| Tannin (mg/ml) | 23.30 ± 2.23 | 20.72 ± 1.68 | 19.02 ± 4.59 | - | - | - | - | - | - | 23.30 ± 2.22 | 1.68 ± 1.68 | 4.60 ± 4.59 |
| species | n = 8 | n = 6 | n = 4 | n = 0 | n = 0 | n = 0 | n = 0 | n = 0 | n = 0 | n = 9 | n = 6 | n = 4 |

### 3.4.5 Relationship of various plant chemical compounds with grazing preference and palatability

A principal component analysis was used to determine the relationship between chemical compounds and rank preference in order to determine those compounds that may influence palatability and thus preference. The results showed that there were no obvious groupings of plant characteristics due to inconsistent relationships observed between most chemical characteristics and rank preference for the different seasons and grazing intensities (Figure 3.6 – 3.7). Low protein, high fibre and high tannin concentration were not positively related to an increase in palatability and preference as hypothesized.

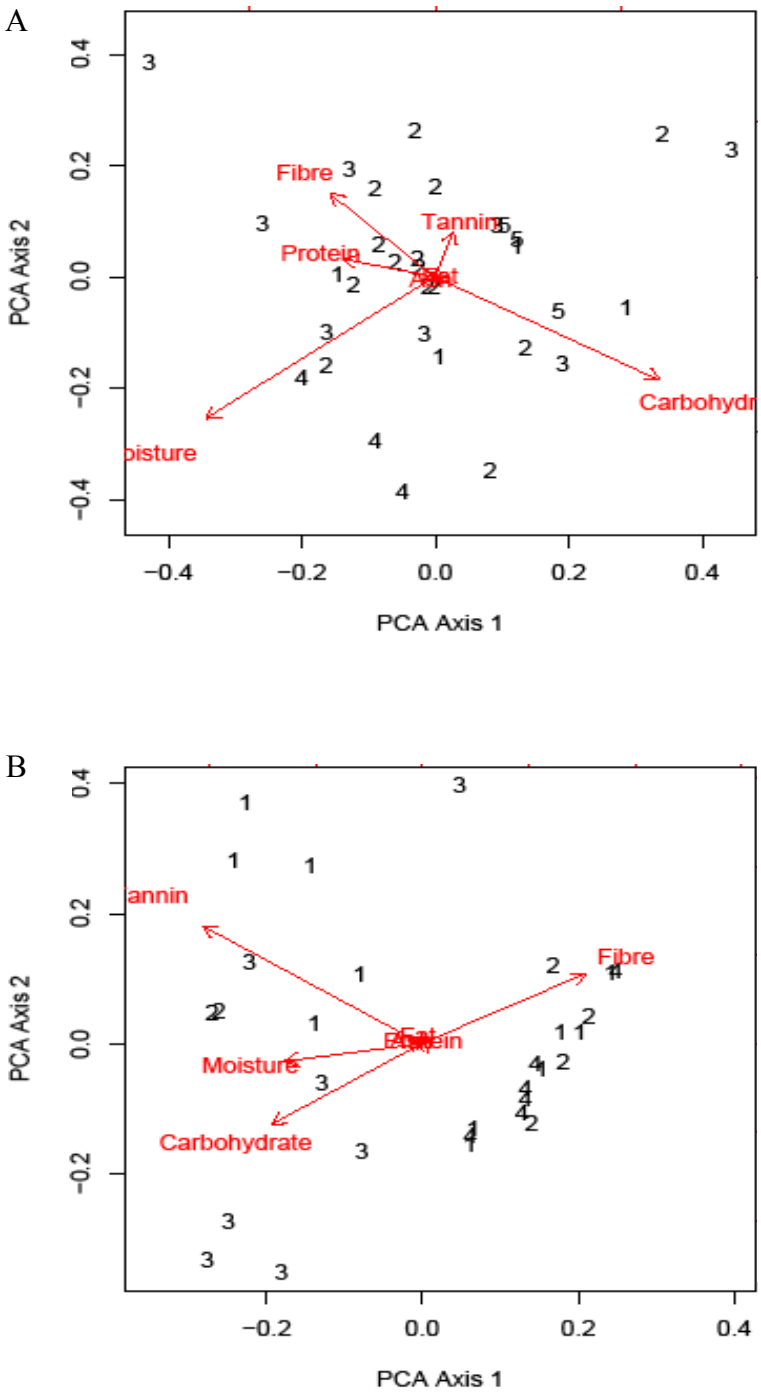


Figure 3.6: Principal Component Analysis of nutrient content at the high grazing site in winter (A) and spring (B). Numbers indicate preference ranked of various grazed species (1-2 = highly preferred; 3= moderately preferred; 4-5 = avoided).

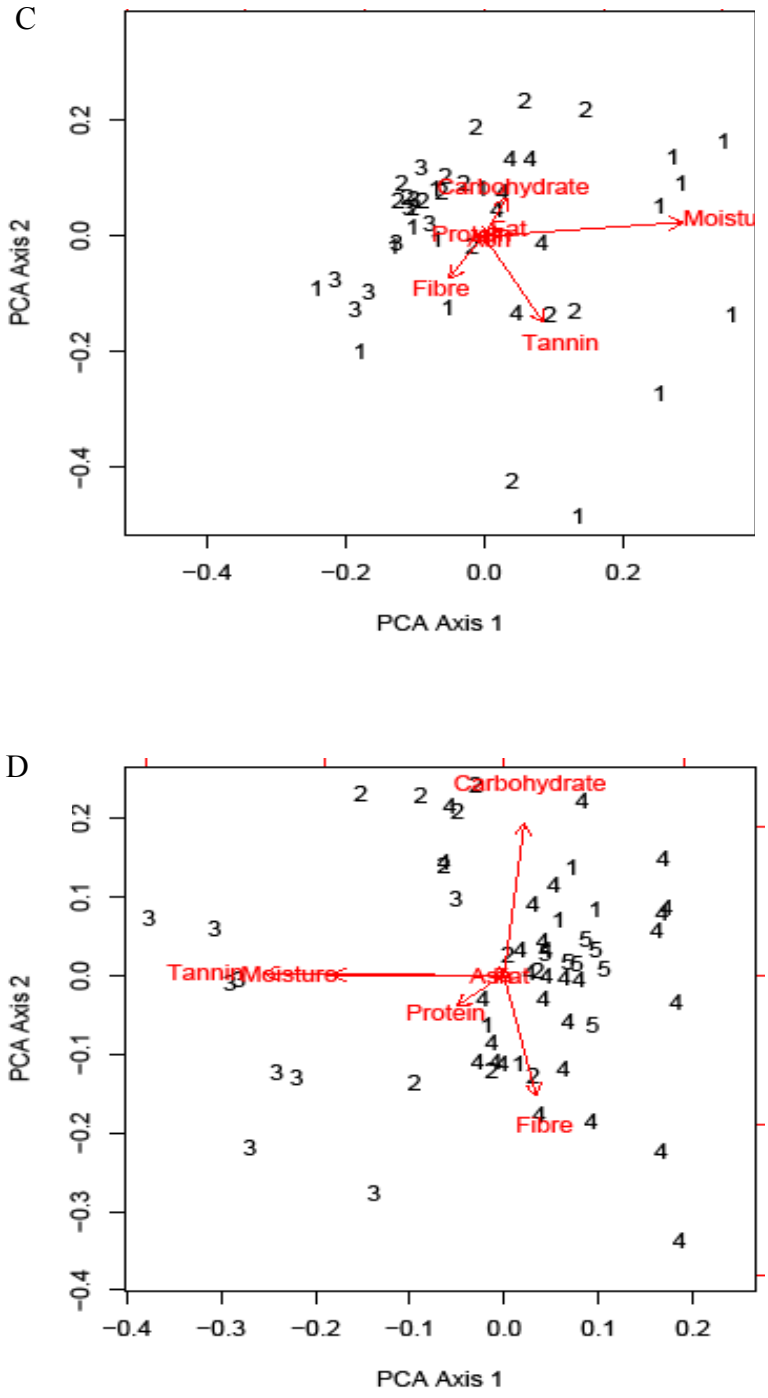


Figure 3.6: Principal Component Analysis of nutrient content at the high grazing site in summer (C) and autumn (D). Numbers indicate preference ranked of various grazed species (1-2 = highly preferred; 3= moderately preferred; 4-5 = avoided).

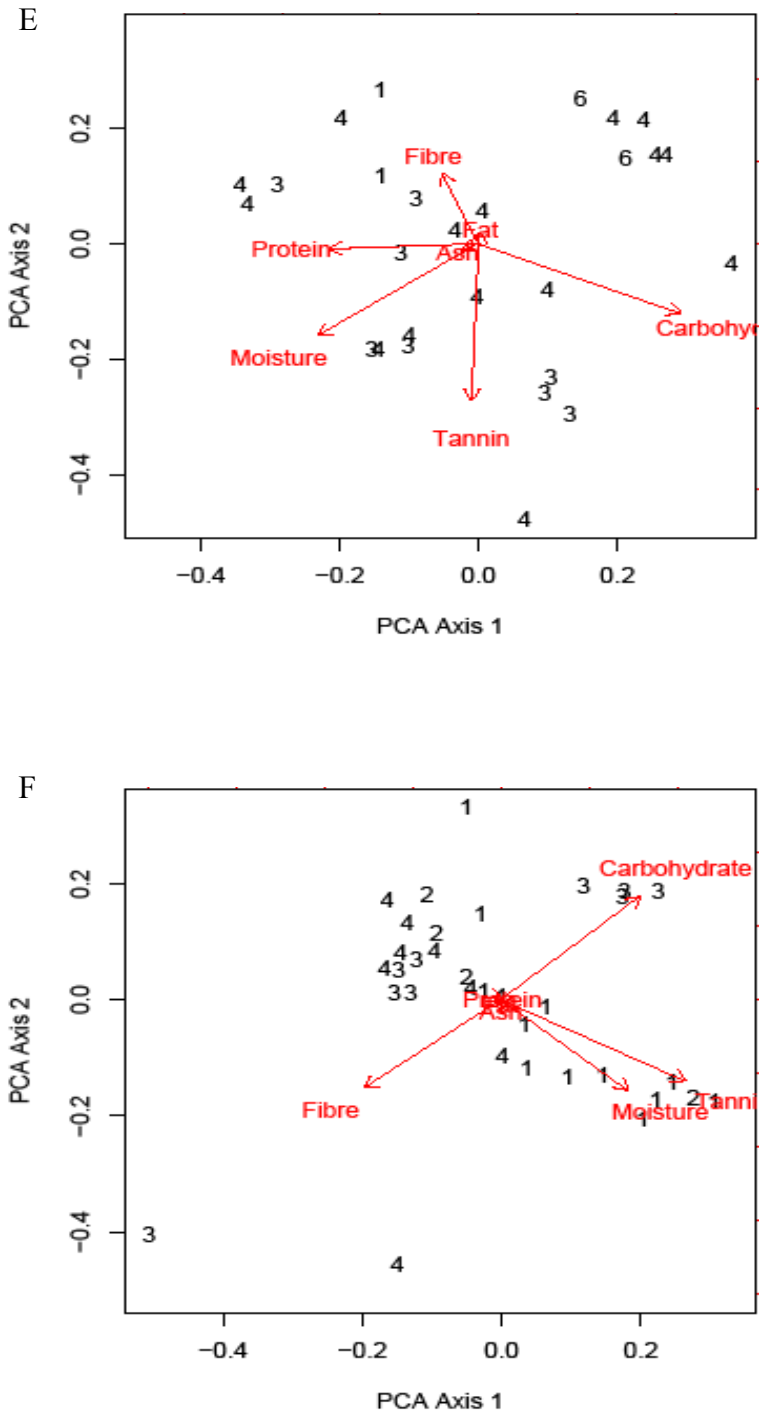


Figure 3.7: Principal Component Analysis of nutrient content at the medium grazing site in winter (E) and spring (F). Numbers indicate preference ranked of various grazed species (1-2 = highly preferred; 3 = moderately preferred; 4-5 = avoided).

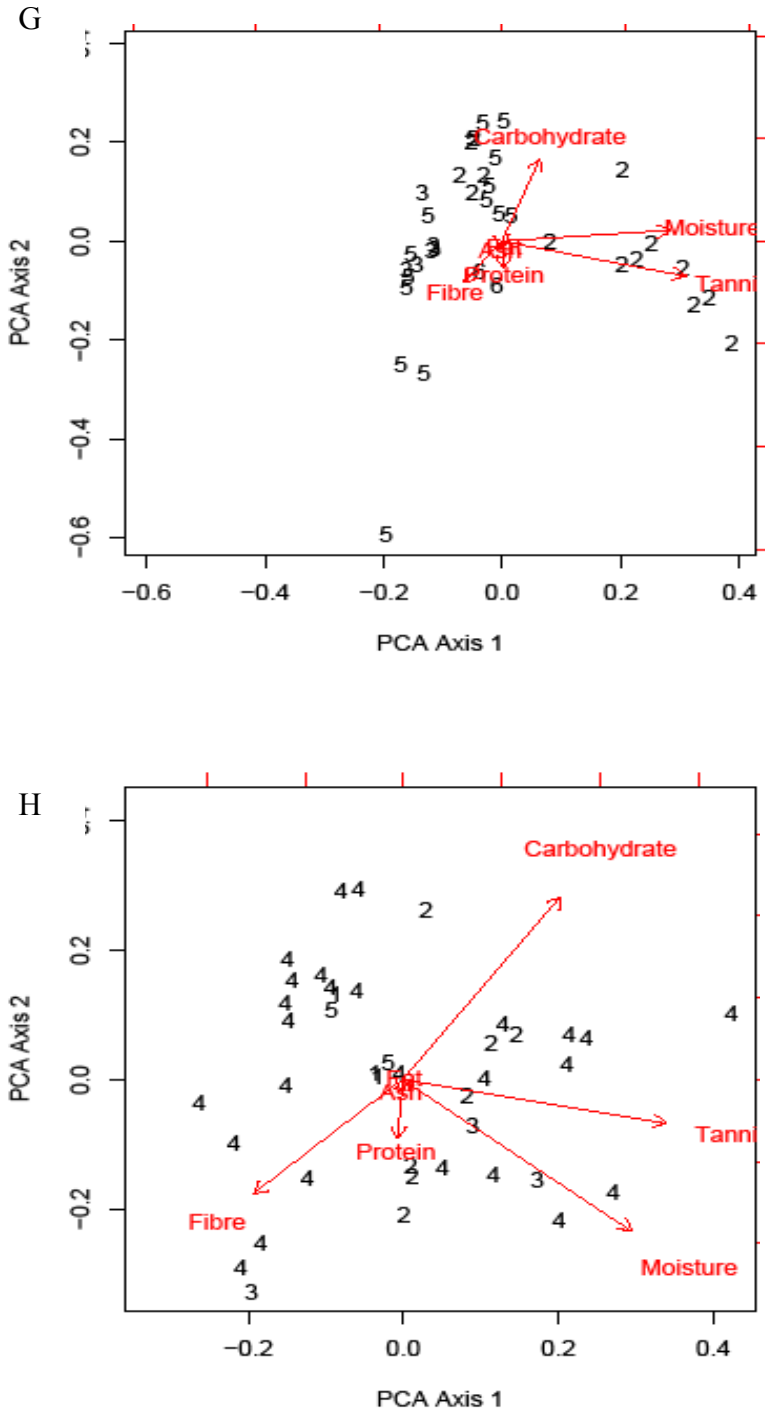


Figure 3.7: Principal Component Analysis of nutrient content at the medium grazing site in summer (G) and autumn (H). Numbers indicate preference ranked of various grazed species (1-2 = highly preferred; 3 = moderately preferred; 4-5 = avoided).

## 3.5 Discussion

The purpose of the study was to investigate variation in plant chemical compounds (crude fat, crude protein, crude fibre, carbohydrate, mineral content, moisture and tannin) and forage preference of large indigenous herbivores in three different grazing intensities. Additionally, the relationship of those various compounds with grazing preference and palatability were assessed. Results showed that there was significant variation in palatability and preference between sites over seasons. In most cases, plant chemical compounds changed as plants matured, coupled with the decrease of preference of large herbivores to a particular plant. My results in part support the suggestion of Georgiadis and McNaughton (1990) that herbivores were able to regulate plant chemical compounds through grazing. The results also showed that under different grazing intensities, plants were able to shift their chemical compounds to deal with the "attacker" (Sankaran & McNaughton, 2005). For example, in winter at the high grazing site, *M. caryophyllacea* had a tannin concentration seven times higher than at the medium grazing intensity.

The relationship between grazing preference and plant chemical compounds showed no consistent relationships between most chemical compounds, preference in different seasons and different grazing intensities**.** These results suggest that forage preference is not driven by fibre, protein and tannin, but by an interaction of multiple compounds at different levels and in different seasons. The patterns observed in this study differed to those reported by Farmer (2005) who found a correlation between plant chemical compounds and grazing preference in the little Karoo of South Africa.

### 3.5.1 Seed germination from dung

Alien grass seedlings were found in high numbers in eland and bontebok dung after seed germination. The high prevalence of alien grass seedlings was the result of the two herbivore species grazing on old fields where these grasses were abundant. Large herbivores are known to disperse seeds via the endozoochory process (Mouissie *et al.*, 2005; Gill, 2006). As a result, alien grass seeds were dispersed to natural vegetation from adjacent old fields by animals that roam freely throughout the different vegetation. Alien species perform better in the community they invade by exerting a strong negative competition on the native herbaceous community (Pivello *et al.*, 1999). Consequently, indigenous grass dispersal in the natural vegetation in the study area might be reduced in favour of alien grasses. A study conducted by Vlok (1988) on lowland fynbos herbs of South Africa in areas infested by alien showed that

alien species posed a threat to the indigenous annuals and geophytes. This lead to the conclusion that endemic flora might become extinct if the spread of aliens increases in abundance in the indigenous vegetation (Vlok, 1988). One of the criteria of that study was the exclusion of domestic livestock grazing during the last growing season. This criterion demonstrated that even though large herbivores are excluded for a short period, the alien grasses were still invading that area. Therefore, in a system such as the fynbos-renosterveld mosaic investigated, where large indigenous game move liberally miles away from alien seed sources (e.g. old fields), the likelihood of alien species to colonize the remaining fragments might increase. Shiponeni and Milton (2006) demonstrated that indigenous herbivores dispersed alien grasses from old fields to natural vegetation. Therefore, the presence of indigenous herbivores maintains and facilitates the propagation of alien grasses within the system because it is well know that seed dispersal is an important mode of plants to colonize new areas (Willson & Traveset, 2000).

However, based on Walton (2006) observations, that under high grazing intensity alien grass species richness in natural vegetation decreased, but increased in ploughed areas. Large indigenous herbivores might decrease alien grass species richness in natural vegetation. Therefore, the survival of alien species in presence of large herbivores and the other modes of seed dispersal in fynbos and renosterveld vegetation types is questionable, and may explain the high alien species richness at the low grazing site.

Despite the fact that restoration projects have been carried out to facilitate re-establishment of indigenous species on old fields (Midoko-Iponga, 2004; Memiaghe, 2008), there are uncertainties whether the herbivores would be able to exist in these small remaining patches without the alien grass species. Alien grasses are known to out-compete indigenous grasses (Daehler, 2003) and spread rapidly into fragmented landscapes (Sakai *et al.*, 2001). In fynbos and renosterveld vegetation, alien grasses out-compete indigenous annuals and geophytes, which form a significant part of species diversity (Milton, 2004). At the study site, alien species *V. myorus* and *Lolium sp.* are highly preferred by herbivores compared to indigenous palatable grasses such as *T. triandra*. This constitutes an obstacle for indigenous species to re-colonise and spread effectively within the remaining patches as well as the old fields. Shiponeni and Milton (2006) argued that alien plants in renosterveld contributed negatively towards the re-establishment and the restoration targets because they can exist for many years in abandoned old-fields. Therefore, the negative effects of alien grass species decreased the rate of recovery of the indigenous grass species. However, the natural vegetation possesses

species such as *C. dactylon*, *H. hirta* and *Eragrostis sp.*, which are highly preferred by herbivores. Those species might be able to provide the nutritional requirement of indigenous herbivores in the system and could enable them to survive (Aregheore *et al.*, 2006).

### 3.5.2 Positive response of plant species to grazing

In this section, three issues related to herbivory are discussed: the impact of grazing on plant palatability (plant chemical compounds), the feedback of palatability on preference, and the effect of seasonal change on both palatability and preference.

Plants under different grazing intensity respond differently to herbivores (Paige, 1992). The carbohydrate value of indigenous grasses *T. unioleae* and *H. hirta* tended to be higher at the high grazing site than at the low grazing site. This could be explained by the fact that the grasses might be grazing-tolerant (Oesterheld & McNaughton, 1988; Danckwerts & Teague, 1989; Sankaran & McNaughton, 2005), which means that they have developed ways to cope with the "attacker" in order to survive damages caused by them (Danckwerts & Teague, 1989). The rate of re-growth and plant fitness is known to be enhanced and promoted by herbivory (Pollet & Detling, 1988; Vallentine, 1990; Agrawal, 2000). Having that ability, plants are able to increase their fitness by producing more carbohydrates when they are grazed (Danckwerts, 1993). However, *I. capensis* showed an interesting trend. This species had a higher concentration of carbohydrate at the medium and low grazing sites compared to the high grazing site in spring and summer. This trend could be linked to the fact that this species is grazing tolerant to up to a certain level of grazing above which its fitness decreases.

### 3.5.3 Negative response of plant species to grazing

While some grass species in the system are tolerant to grazing, other species, such as *Ficinia sp.* and *M. caryophyllacea*, tend to invest more in defence mechanisms through the production of high concentrations of condensed tannin at the high grazing site than at the low grazing site. Defoliation by grazing increases the concentration of anti-palatable chemical compounds that aim at preventing the plant from being eaten or overutilized (Ras, 1990; Van Hoven, 2002). Even though tannin has the attribute to deter herbivore attacks (Launchbauch *et al.*, 2001), it did not decrease the preference of grazers to *Ficinia sp*. This is probably because *Ficinia sp.* also had a high concentration of crude protein that might alleviate the negative effect of tannin. For example, in the Limpopo Province of South Africa, the composition of high condensed tannin levels of *Colophospermum mopane* species did not seem to create a limiting browse consumption by Kudu (*T. strepsiceros*) (Hooimeijer *et al*., 2005). However,

the combination between high crude protein levels and tannin content seem to be the alternative explanation of *C. mopane* consumption by Kudu (Hooimeijer *et al*., 2005). The question whether herbivores have alternatives in such a system where food becomes scarce during autumn and summer is pertinent since the cover of grasses, restios and sedges diminishes significantly during that time of the year (personal observation). For example, the cover species such as *I. capensis* decreased from over 2 % in spring to 1% later in the year. During the active growing season, when herbivores are surrounded by abundant food, this species was avoided. However, in the later seasons, when food was scarce, *I. capensis* became highly preferred even though the concentration of condensed tannin at that stage was higher. In contrast, Cooper and Owen-Smith (1985) reported that in the northern Transvaal bushveld of South Africa, forage plants with high tannin content tend to be rejected as food by ungulates. Apparently, the concentration of condensed tannin, the season of the year and the type of species grazed might play a role in the selection by herbivores. Therefore, tannin on its own cannot explain plant herbivore preference, because these herbivores were in an environment composed of an heterogeneous vegetation (Belovsky & Schmitz, 1991), and the amount of tannin ingested by the herbivores in the system might be dosage dependent (Freeland, 1991). Thus, the amount of tannin produced was not efficient to repel herbivores, especially when the food became scarce.

Nevertheless, it is also possible that herbivores in the system have developed or possess natural strategies to escape those defences (McArthur *et al*., 1991). For example, in their study on the effect of saliva protein on tanniferous forage, Robbins *et al*. (1987) found that the complex salivary proteins produced by herbivores bind tannins in a specific mode and reduce the toxicity of tannin. Belovsky and Schmitz (1994) stated that there is no type of plant defence that could be certain to decrease plant consumption. This is because defence effectiveness depends upon other qualities of the defended plant as well as on the quality of other plants available to the herbivore within the environment (Belovsky & Schmitz, 1994). Consequently, moisture, carbohydrate or protein content could have been maintaining the high palatability of *Ficinia sp.* and therefore the preference of the herbivores in autumn and winter.

### 3.5.4 Grazing intensity effects on plant palatability

The intensity of grazing had no effect on the mineral and crude fat content in the study, except for *M. caryophyllacea* and *T. unioleae*, in which crude fat was found to vary in autumn. In general, *T. unioleae* crude fat tended to be higher at the high grazing site than at the low

grazing site, while crude fat content of *M. caryophyllacea* showed trends in the opposite direction. Literature on the effect of large herbivores on crude fat is poorly documented, therefore no clear explanation can be offered for the effects on grazing intensity on crude fat. Based on the results observed, the response of species, with regard to crude fat to grazing intensity, is likely species related.

Concerning water content, crude protein and crude fibre; the results are aligned with the findings of Georgiadis and McNaughton (1990). High grazing intensity increases water content, crude protein and crude fibre. For example, in the present study, the water content of *M. caryophyllacea* in spring during the juvenile actively growing stage is higher at the high grazing site than at the low grazing site, but decreases in summer and in autumn. Furthermore, it was found that the crude protein content of *Ficinia sp.* was promoted through high grazing. The same observation was reported by Ainalis *et al*. (2006), when they studied the effects of grazing on forage quality of woody and herbaceous species. They found that the level of crude protein of foliage was relatively higher when plants were grazed upon, compared with non-grazed foliage. This observation could be linked to the result made in section 3.5.2 with regards to the increase of carbohydrate as related to grazing. From these observations, I conclude that grazing promotes palatability of herbage at least for some plant species.

### 3.5.5 Plant palatability and seasonal variation

Palatability varies through the seasons, resulting in change of the herbivore preferences (Danckwerts & Teague, 1989). *I. capensis,* which had showed similar trends in chemical composition as *M. caryophyllacea,* confirmed that depending on the season and the species grazed, each compound could display different characteristics. In winter, *I. capensis* is totally avoided, although it had a higher crude protein content at the high grazing site than at the low grazing site, but became gradually highly preferred in spring and summer. This suggests that plant species germinating in spring may become less preferred in winter. This observation is contradictory with the statement made by Theron and Booysen (1966) that species such as *Tristachya hispida*, *Setaria perennis* and *Themeda triandra* were more preferred with advanced maturity. The explanation could be that this species, as was found for *T. triandra,* became highly palatable at a specific stage of its growth (Danckwert & Teague, 1989), because as a plant matures, the physiology of the grazed plant changes (Larcher, 2003). For example, Dabo *et al*. (1988) investigated the effect of maturity on the chemical composition of grass. They found that maturity had a great effect on the concentration of all the chemical constituents. Kilcher (1981) reported that plants show a decreasing nutrient concentration

with advancing growth towards maturation. Therefore, plant maturation has a significant effect on herbivore preference (Theron & Booysen, 1966).

To understand the seasonal change of tannin concentration related to leaf age, Du Toit (1992) investigated the presence of tannin on various African grass species. He found that tannin concentration was correlated with leaf age, i.e. mature leaves contained more tannin. The maximum tannin production occurred in winter while the regrowth stage had the lowest tannin production. Results of this study converged in regard to the high concentration of tannin in winter for *Ficinia s*p. and *M. caryophyllacea,* but diverged from it with the regrowth stage having the lowest tannin concentration.

### 3.5.6 Relationship between preference and plant palatability

The results indicate that in fynbos and renosterveld, the relationship between preference and plant chemical compounds are not consistent, since no patterns were found to explain clearly what compounds might drive preference. However, it is also possible that a combination of chemical compounds could be the reason for the selection by the grazers (Heady, 1964), or other compounds not included in the present study would influence the forage selection by a herbivore. The results of the study with regard to the role played by the concentration of condensed tannin are similar to those reported by Cooper and Owen-Smith (1985), that other factors besides condensed tannins affect food selection by these ungulates. Wambolt's (2004) findings indicated that crude protein did not have a primary role in determining preference as I hypothesized. Based on crude protein content, he realized that the most palatable plant species was the least preferred and the least palatable was the most preferred. Therefore, other factors such as environmental parameters may play a role in the palatability and preference relationship (Danckwert & Teague, 1989).

### 3.6 Conclusion

In summary, I conclude that grazers such as eland tend to move alien grass seed from old fields to natural vegetation (Shiponeni & Milton, 2006), The solution for reducing the spread of alien grasses into the remaining natural fragment should be focused on the increase of incentives towards restoration goals of the abandoned old fields as they constitute a source of alien species.

Grazing affects plant palatability through its variable effect on plant chemical content. It decreases or maintains palatability through the production of condensed tannin of the grazed plant. My results agree with the conclusion by Barroso (2003), who found that stocking rates affect plant palatability. Tannin, crude fibre and carbohydrate concentration vary under different grazing intensities. However, these differences were species related and plant age dependant (Hester *et al.*, 2006). Some species containing high levels of condensed tannin were equally grazed and highly preferred by grazers. Therefore, grazing management requires an understanding of the biochemical, physiological and behavioural mechanisms that mammals use to counteract the plant defence mechanism in a forage system (Bryant *et al.*, 1992). The fact that species such as *I. capensis* were observed having a seasonal shift in forage preference implies that the phenological aspect of some grazed species under special circumstances need to be investigated further (Kassa *et al*., 2007). More work needs to be carried out on the diet of grazers as they might mix their food intake when a food became scarce to counteract the effect of high tannin ingestion. Two categories of plants were observed: Those that are grazing tolerant and produce more carbohydrate when grazed (*Hyparrhenia hirta; Tribolium unioleae*), and those that are grazing intolerant and produce chemical compounds to deter herbivore damages (*Ficinia sp.; Montinia caryophyllacea*).

This study found no evidence to suggest that high plant palatability is related to high crude protein, low fibre and low tannin concentrations. Therefore, forage preference cannot be linked to the absolute levels of nutrients and antifeedant compounds, other than on the ratio of those nutrients and antifeedant compounds (Katjiua, 2006). Characteristics not taken into account in this study could play an important role in determining palatability and preference such as specific minerals, e.g. calcium and potassium (Lee, 1988), specific fibres such as cellulose and hemicellulose (Georgiadis & McNaughton, 1990) or soil physical and chemical properties. This study contributes to the understanding of the complexity of plant animal interaction in a fynbos-renosterveld mosaic and leads to the conclusion that a combination of

plant chemical compounds at a specific period results in herbivores preference in the area. Farmers need to pay attention to the nutritional status of plant species grazed to know whether they meet the nutritional requirements of the game in the area for a better grazing management (Taylor & Ralphs, 1992). Elandsberg provides the best stocking rates for effective grazing management and this results in lower tanniferous compound production compared to Krantzkop.

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# Chapter 4: Effects of grazing intensity/stocking rate on soil properties in an Alluvium Fynbos-Renosterveld mosaic.

## 4.1 Introduction

Soil is the principal basis upon which plants root and absorb nutrients for growth and fitness. In farming, the knowledge of soil and especially its chemical properties is crucial for plant productivity (Widmann *et al.*, 1990; Phillips-Howard & Lyon, 1994), plant physiological status (Chunlong *et al.*, 2008) and game production (Ebedes & van Rooyen, 2002). However, these properties are subjected to variations under the presence of large herbivores and their grazing intensity, especially in rangeland and grazing management practise (Schuman *et al*., 1999; Sankaran & Augustine, 2004). Thus, the presence of herbivores such as domestic livestock or indigenous game influences or modifies soil properties in a particular system (Xu *et al.*, 2007).

In systems such as the fynbos and renosterveld in the South-Western Cape of South Africa where the landscape has been severely transformed due to farming, it is crucial to investigate the effect of grazing intensity on soil properties. Rebelo *et al*. (2006) reported that the impact of large game on the fynbos biome has been a neglected topic, and almost no information is available on the impact of large herbivores on soil characteristics in the remaining natural vegetation. Herbivores graze plants within this system to fulfil their daily nutritional needs, and plants provide them with nutrients that may or may not meet their nutritional requirements for their growth and fitness, depending on soil chemistry and nutrient status. Soil properties of importance include pH, soil moisture content, carbon to nitrogen ratio, available nitrogen and available phosphorus.

Soil pH is the measurement of ion $H_3O^+$ in a soil solution, i.e. the alkalinity and acidity of the soil solution. This property controls nutrient availability and is affected by the water regime and soil organic matter decomposition through the release of organic acids (Hayes, 1991; Bardgett, 2005). It has been shown that an increase in rainfall triggers a decrease in pH through nutrient leaching (Black, 1957; Bohn, 1979), and grazing intensity causes the variation of pH (Walters & Martin, 2003). For example, Hatton and Smart (1984) reported that in the Chobe region of Murchison Falls National Park, Uganda, the removal of large

herbivores resulted in an increase in soil pH. Conversely, pH affects litter decomposition of organic matter (i.e. nitrate release is more rapid in neutral soil than in acid soil). For example, neutral soil increases decomposition whereas acid soil decreases the break down of organic matter (Etherington, 1975; Bohn, 1979).

Water is a source of life to all living organisms and is the component with which nutrients are transported from the soil to the root system in plants. Therefore, a depletion of water will be followed by depletion in nutrient uptake and a change in the physiological state of plants (Etherington, 1975). For example, under low soil moisture, seedlings of *Terminalia sericea* in a nursery experiment at the Forestry Research Station in Okahandja, Namibia, were recorded to have a higher condensed tannin concentration than under a high water treatment (Katjiua & Ward, 2006). A reduction in soil water content further affects soil organic matter decomposition, as under dry conditions, soil decomposition of organic matter is reduced (Jenkinson, 1981). Additionally, studies have shown that soil moisture content decreased with an increase in grazing intensity (through trampling action by herbivore hooves) (Dormaar *et al.*, 1989; Walters & Martin, 2003).

The carbon to nitrogen ratio describes the amount of carbon relative to the amount of nitrogen in the soil. This ratio has a controlling effect on the decomposition of tissue in the soil (Ruess & McNaughton, 1987), and determines the ability of bacteria to decompose organic matter (Lavelle & Spain, 2001). Soil with a high carbon to nitrogen ratio has a low decomposition rate, whereas soil with a low carbon and nitrogen ratio has a high decomposition rate (Ruess & McNaughton, 1987). Furthermore, the carbon to nitrogen ratio can vary with rainfall, temperature and soil type amongst others (Snowdon *et al.*, 2005).

Nitrogen is of importance to all living organisms on earth. It is one of the main essential compounds for the biosynthesis of protein and is the limiting factor in plant growth. Two categories of nitrogen can be classified according to their nature: organic nitrogen (forming the building blocks of living organisms) and inorganic nitrogen (product of mineralization) (Satchell, 1974; Lavelle & Spain, 2001). In this study, particular attention was focused on mineral nitrogen. Mineral nitrogen is the product of decomposition of organic matter via microbial activities (Gyllenberg & Eklund, 1974). This has been reported to be enhanced by herbivores through dung and urine deposition (Ruess & McNaughton, 1987; McNaughton *et al.*, 1997). Under natural conditions, nitrogen can be found in a soil solution as ammonium nitrogen ($NH_4^+N$) or nitrate nitrogen ($NO_3^-N$) (Haynes & Goh, 1978). Ammonification (transformation of organic nitrogen to ammonium) and nitrification (transformation of

ammonium to nitrate) is lowered when the temperature decreases (Black, 1957). Furthermore, the nitrifying micro-organisms decrease their activity with a decrease in soil pH (Etherington, 1975).

Phosphorus is a compound found in protein and is essential for all plant growth and fitness. It is involved in a multitude of biological processes and constitutes a limiting factor to plant growth (Bardgett, 2005). In the soil solution, the phosphorus is available to plants in the form of orthophosphate $H_2PO_4^-$ or $HPO_4^{2-}$ (Lavelle & Spain, 2001). Walters and Martin (2003) showed that the grazing intensity increased the phosphorus content in the soil. In addition, it may be noted that phosphorus availability to plants is relatively low in acidic soil and increases at a pH of about 6 to 7 (Bardgett, 2005).

However, the question remains on the relationship between plant quality, soil properties and the health of herbivores. Herbivores feeding in a nutrient-poor habitat can suffer from nutrient deficiencies, poor digestibility (Wolfson, 2002), and toxicity (Van Hoven, 2002), or can be exposed to diseases (Du Toit *et al*., 2002; Meissner, 2002). Therefore, the knowledge of soil properties constitutes a fundamental part of game management and can reveal insights into an alternative supplement feeding of herbivores.

This chapter aims at investigating the effect of three different grazing intensities (low, medium and high) on soil properties (pH, moisture, carbon to nitrogen ratio, ammonium and nitrate) in an attempt to provide useful guidelines for the grazing management in a Fynbos-Renosterveld mosaic. While it must be acknowledged that there is a potential pseudo-replication problem in the observational design of this project, the following question is addressed:

1- How do soil properties vary between different grazing intensities?

My hypotheses are that:

- Significant differences among the values of soil parameters studied will be observed between different grazing intensities.
- pH values will be lower in winter whereas moisture will be the highest in winter at all sites.

- Moisture will be the lowest on the high grazing site compared to the low and medium grazing site, whereas pH will be the lowest at the high grazing site compared to the low and medium grazing sites.
- The carbon to nitrogen ratio will be higher at the high grazing site in comparison to the low and medium grazing sites.
- Phosphorus and nitrogen available in the soil will be higher at the high grazing site than at the low and medium grazing sites.
- Moisture will be the main factor influencing the concentration of phosphorus and nitrogen available in the soil.

## 4.2 Methods

### 4.2.1 Soil samples collection

Soil samples (600 grams) were collected on ten plots each at Voëlvlei (hereafter referred to as low grazing intensity), Elandsberg (hereafter referred to as medium grazing intensity) and Krantzkop ammunition factory (hereafter referred to as high grazing intensity). Samples were collected in open area with a hand soil auger in the middle of each plot (20 m x 50 m) used for plant surveys. The collections were made at a fixed sampling depth of 20 cm as this includes the full root biomass (Boone *et al.*, 1999), and the sampling area spot was 50 cm x 50 cm centimetres. Samples were bulked in order to obtain a homogenous sample and stored in closed plastic bags at approximately 4 ºC until further analysis. Collections were performed seasonally at the same locations from November 2006 to September 2007.

### 4.2.2 Soil sample laboratory processing.

The soil samples were air-dried at ambient humidity and temperature. They were then broken up and sieved to pass through 2 mm to obtain subsamples and to exclude large particles that were less reactive (Boone *et al.*, 1999). Each sample was then subjected to the following analysis:

#### 4.2.2.1 pH

The pH was potentiometrically determined in the supernatant suspension of 1:2.5 soil-liquid. The liquid was 1 *M* KCL and the laboratory method applied was that of Tan (2005).

4.2.2.2 Moisture

Soil moisture was determined on a oven-dry basis (Boone *et al.*, 1999). Ten grams of fine earth was measured into a tare moisture tin (weighed with microbalance at 0.001 accuracy). The sample was dried overnight at 105ºC, removed from the oven the following day, cooled down and weighed. The following equation was applied to determinate the percentage of moisture.

$$\text{Moisture content (\%)} = \frac{\text{(weight of wet soil + tare tin)} - \text{(weight of dry soil + tare tin)}}{\text{(weight of dry soil + tare tin)} - \text{(tare tin)}}$$

4.2.2.3 Carbon and nitrogen ratio

This analysis was conducted by the Department of Soil Sciences at Stellenbosch University. The dry-combustion C and N (CN) analyzers sample at high temperature method was used following Elliot *et al.* (1999).

4.2.2.4 Available nitrogen and available phosphorus

Phosphorus and nitrogen availability was respectively determined by Bray and Kurtz (1945) and Bremner (1965). This procedure was conducted by Bemlab$^{BK}$ (AECI Building W21, De Beers Street, Somerset West, South Africa).

4.2.3 Statistical analysis

Statistical analyses were performed in STATISTICA 8 (Statsoft, Inc. 2007). To test for an interaction between grazing intensity and seasonal variation of soil pH levels (Figure 1), soil moisture variation (Figure 2), soil ammonium concentration (Figure 4), soil nitrate concentration (Figure 5) and soil phosphorus concentration (Figure 6), a factorial ANOVA was used. A one-way ANOVA procedure was used to determine the effect of grazing intensity on the soil carbon to nitrogen ratio (Figure 3). When interactions were non-significant and the residuals where not normally distributed, a boostrap analysis was performed. Carbon to nitrogen ratio was estimated once, whereas available phosphorus and available nitrogen were estimated twice, for winter and summer.

**4.3 Results**

The study design has constraints; the grazing intensity is super-imposed on a potential soil gradient. However, sites selected are of the same vegetation type defined through soil and climate (Rebelo *et al.*, 2006). Alternative explanations for soil variation might exist (i.e. not

driven by grazing patterns). The following results explore patterns and potential explanations for them.

### 4.3.1 Soil pH

Soil pH (Figure 4.1) values were significantly higher at the medium grazing site than at the high grazing site during winter ($F_{6,\ 107}$ = 1.531, p = 0.033). In autumn, the pH was significantly higher at the low grazing site than at the high grazing site ($F_{6,\ 107}$ = 1.531, p = 0.033). Additionally, the pH value was significantly higher in winter compared to summer at the high grazing site ($F_{3,\ 107}$ = 11.094, p= 0.001). Overall, the soil pH is lower at the high grazing site than at the medium and low grazing site for all seasons.

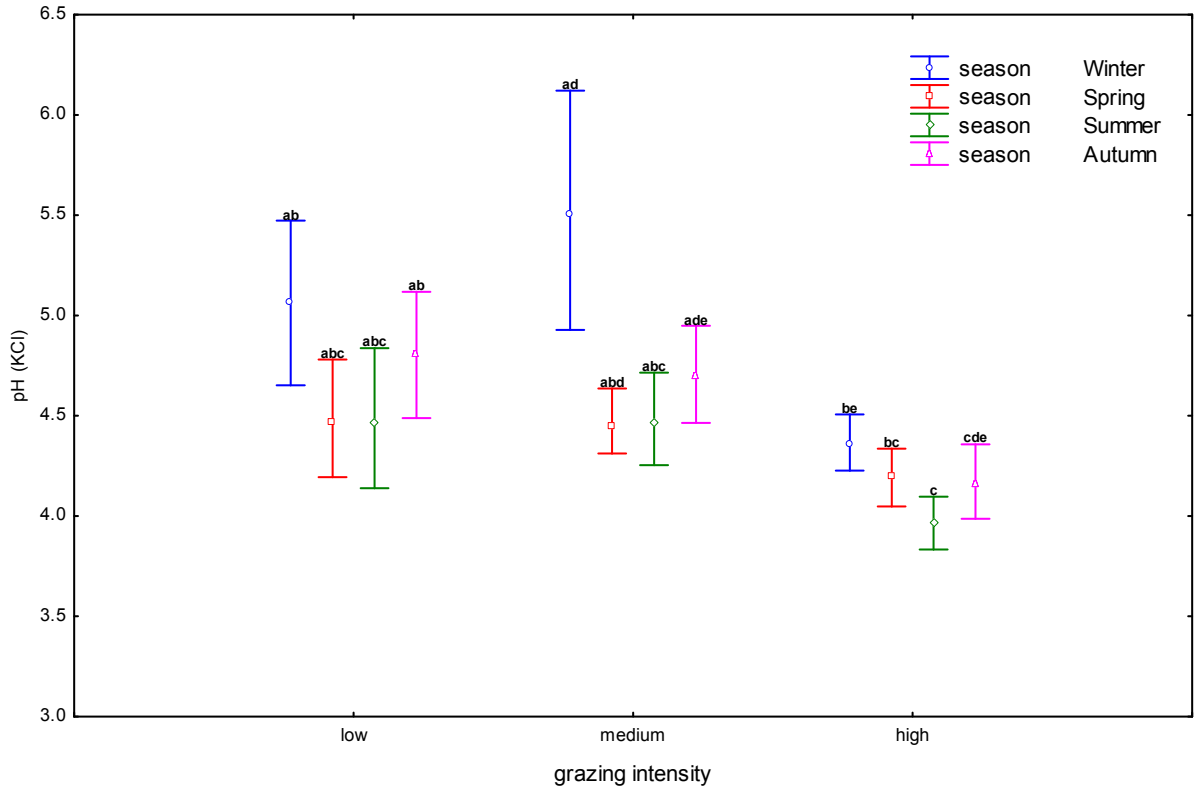


Figure 4.1. Interaction between grazing intensities and seasonal variation on soil pH levels. Different letters indicate significant differences between grazing intensity and seasons. Vertical bars denote 95% confidence intervals.

### 4.3.2 Soil moisture

Moisture was significantly higher at the low grazing site compared to the high grazing site ($F_{6,\ 106}$ = 4.321, p = 0.001) in Autumn (Figure 4.2). At all sites, soil moisture reached its peak during winter and autumn whereas the lowest values were recorded in spring and summer. The values of soil moisture were significantly higher at both the high and low grazing

intensity in winter compared to spring ($F_{6, 106} = 4.321$, $p < 0.001$; $F_{6, 106} = 4.321$, $p < 0.001$). However, no significant differences were observed at the medium grazing site between winter and spring ($F_{6, 106} = 4.321$: $p = 1$). Finally, moisture was significantly lower for all study sites in winter compared to summer ($F_{6, 106} = 4.321$; $p < 0.001$).

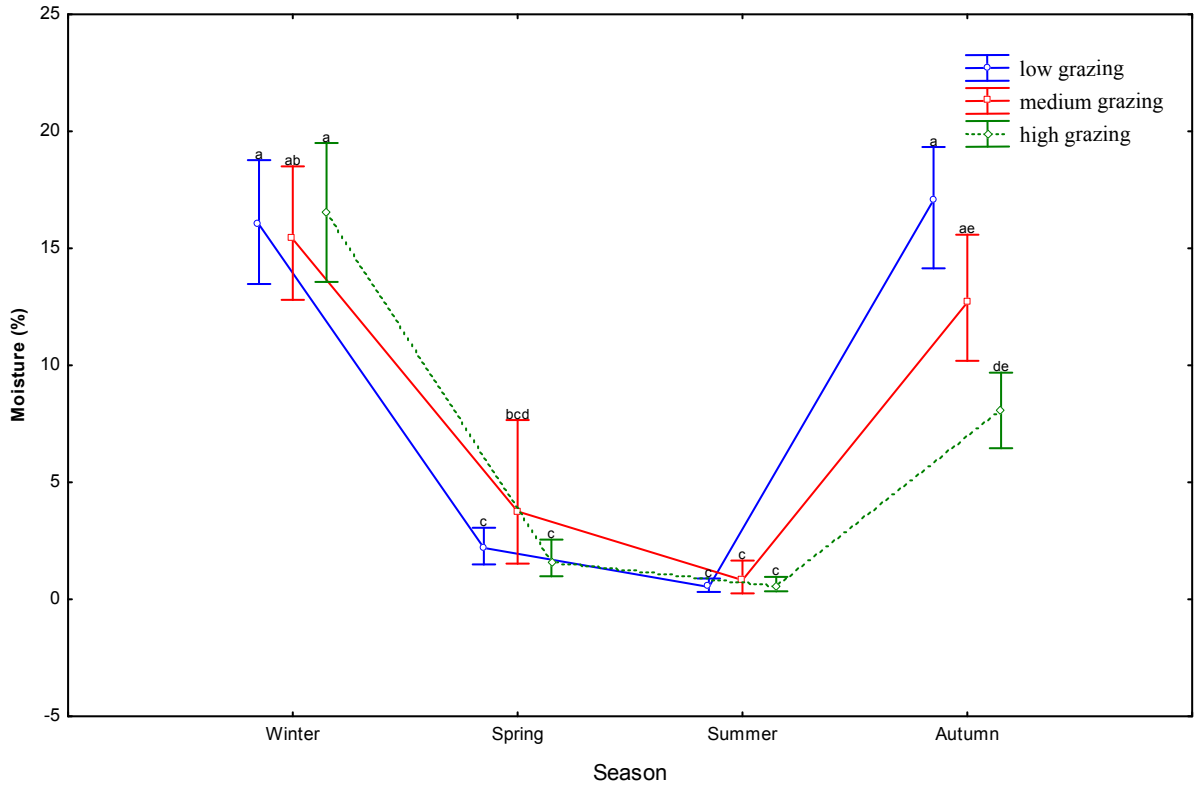


Figure 4.2. Soil moisture variation throughout the year under three grazing intensities. Different letters indicate significant differences between treatments. Vertical bars denote 95% confidence intervals.

### 4.3.3 Carbon to nitrogen ratio

There were no significant differences in the C/N ratio between the three treatment level of grazing ($F_{2, 26} = 0.896$; $p > 0.05$; Figure 4.3).

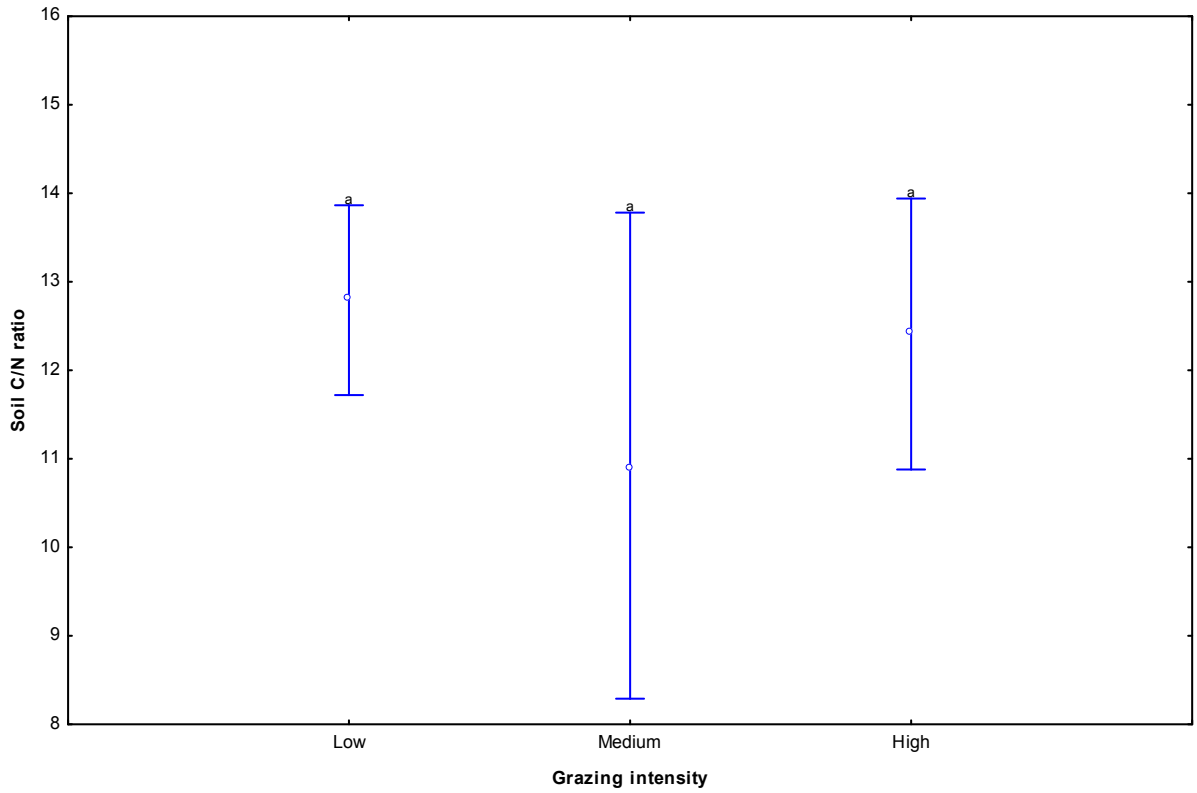


Figure 4.3. Relationship between grazing intensities and soil carbon to nitrogen ratio. Different letters indicate significant differences between treatments. Vertical bars denote 95% confidence intervals.

### 4.3.4 Available nitrogen

#### Ammonium ($NH_4$-N)

The concentration of ammonium showed significant differences between winter and summer at both the low and high grazing site (Figure 4.4). The level of ammonium was significantly higher in winter compared to summer at both the low and high grazing site ($F_{2, 53} = 4.488$, $p = 0.038$; $F_{2, 53} = 4.488$, $p = 0.038$, $p < 0.001$). However, the ammonium concentration in winter of both the low and high grazing site, was significantly higher compared to the medium grazing site ($F_{2,53} = 4.488$; $p = 0.008$; $F_{2,53} = 4.488$, $p = 0.008$). Similar observations were made in summer, where the concentration of ammonium at the low and the high grazing site was significantly higher than at the medium grazing site ($F_{2, 53} = 4.488$, $p < 0.001$; $F_{2, 53} = 4.488$, $p < 0.001$).

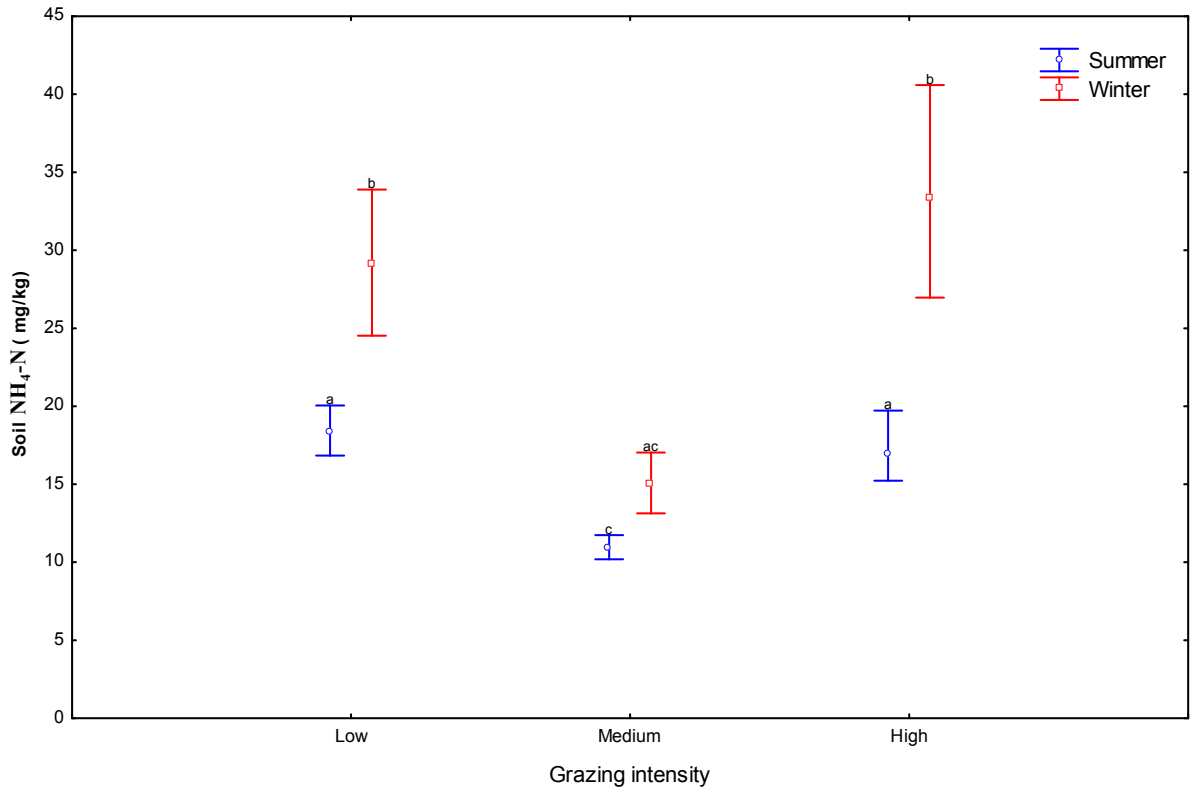


Figure 4.4. Interaction between grazing intensities and seasonal variation in soil ammonium ($NH_4$-N) levels. Different letters indicate significant differences between treatments. Vertical bars denote 95% confidence intervals.

## Nitrate ($NO_3$-N)

The nitrate concentration was significantly different between winter and summer at the low grazing site (Figure 4.5). Nitrate concentration was significantly higher at the low grazing site in winter compared to summer ($F_{2, 53} = 7.518$; $p = 0.022$). However, no significant differences were observed in winter between the low, medium and the high grazing site ($F_{2,53} = 7.518$, $p > 0.05$), while in summer, the nitrate concentration was significantly higher at the high grazing site compared to the low grazing site ($F_{2,53} = 7.518$; $p = 0.008$). Nitrate levels did not change significantly between seasons at the medium and high grazing site.

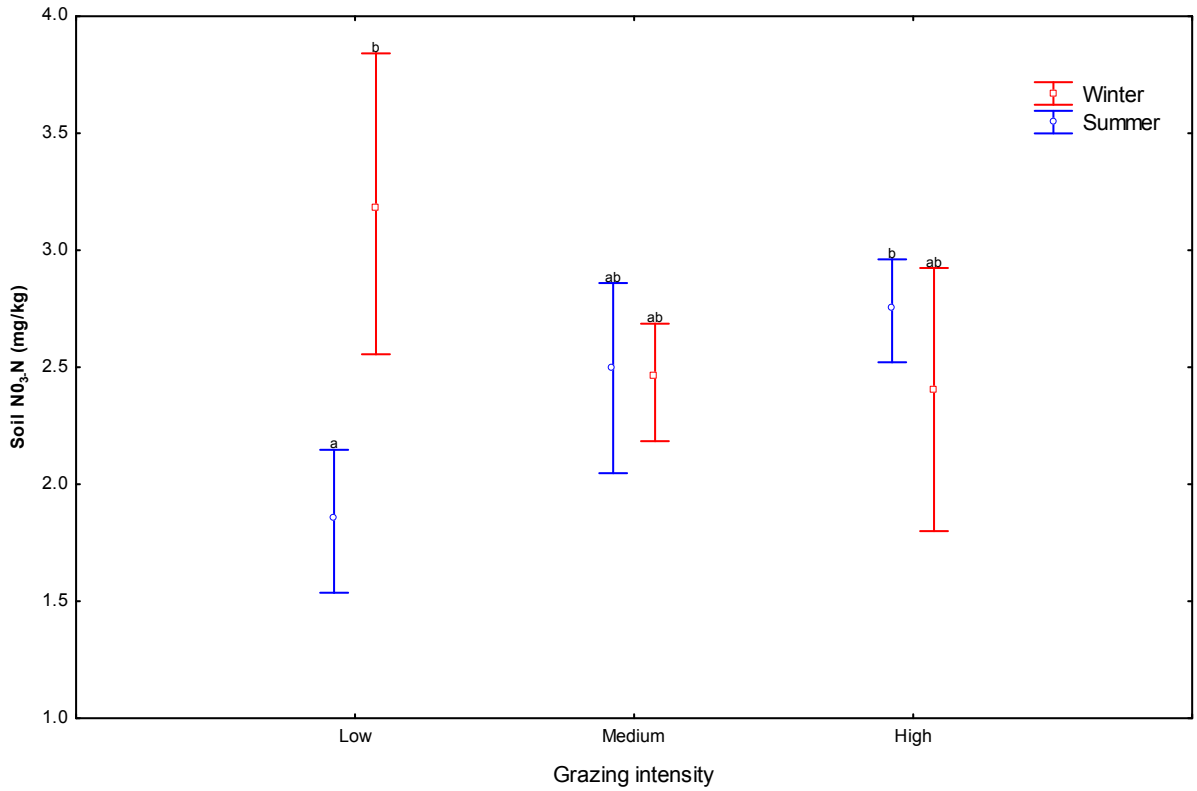


Figure 4.5. Interaction between grazing intensities and seasonal variation in soil nitrate ($NO_3$-N) levels. Different letters indicate significant differences between treatments. Vertical bars denote 95% confidence intervals.

### 4.3.5 Available phosphorus

The concentration of the available phosphorus was significantly higher at the high grazing site in winter compared to summer and between the medium and the high grazing site in winter respectively ($F_{2,52} = 2.484$, $p = 0.008$, $F_{2,52} = 2.484$, $p < 0.001$, Figure 4.6).

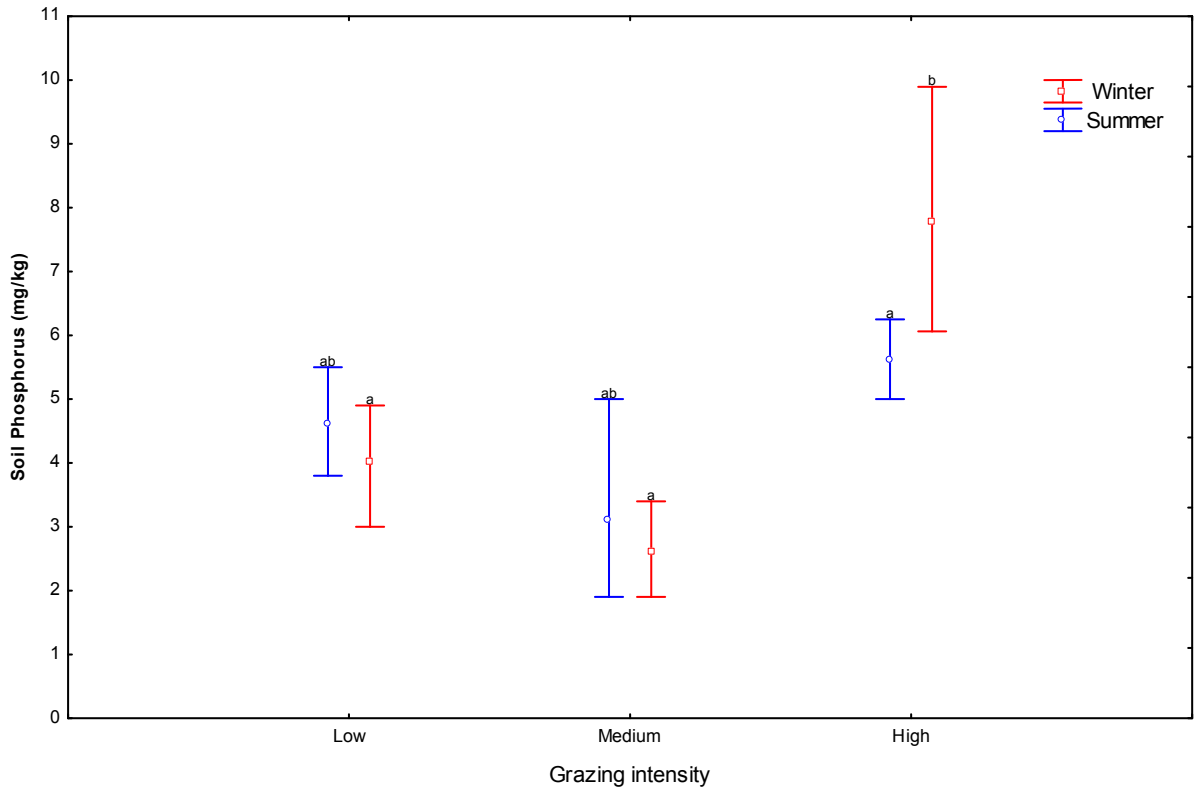


Figure 4.6. Interaction between grazing intensities and seasonal variation in soil phosphorus levels. Different letters indicate significant differences between treatments. Vertical bars denote 95% confidence intervals.

## 4.4 Discussion

With the exception of the carbon to nitrogen ratio, the stocking rate appeared to have had a significant effect on soil properties investigated. However, caution must be applied to the interpretation of the results, since it is not entirely possible to exclude the chance that the observed change may be due to variation in soils between study sites, and not to stocking rate differences. Ammonium, nitrate and phosphorus showed significant variation with grazing pressure. The medium grazing intensity had the lowest ammonium concentration in both winter and summer, while nitrate concentration was more stable under the presence of herbivores. The results found for nitrate concentration in summer are aligned with those of Baron *et al*. (2001) that under heavy grazing the nitrate concentration is higher. Similar to what Owen-Smith's observation in Botswana, that extractable phosphorus was higher where herbivore congregated, were phosphorous levels higher under high grazing in this study.

### 4.4.1 pH and soil moisture

Water is an important element which enables soil nutrients to move between soil particles in order to fulfil plant demands. With the exception for autumn, between the high and the low

grazing pressure, grazing intensity had no significant effect on soil moisture content. Herbivore trampling compacts the soil and reduces the soil pore space at high grazing intensities (Harrison & Bardgett, 2008). During autumn, when the soil is moderately wet, this observation is much more apparent (Owen-Smith, 1999). My results converge with the findings of Knoll and Hopkins (1959), and Holechek *et al.* (1999), that trampling decreases the water soil infiltration rate and thus soil moisture as well, especially at high stocking rates under moist conditions (Warren *et al.*, 1986, Walters and Martin 2003).

The pH value was the lowest at the high grazing intensity regardless of seasonal variation. The results of the present study support the finding of Walters and Martin (2003) that grazing decreases soil pH. This implies that high grazing pressure has an important impact on soil pH. Even though soil pH is influenced by the type of parent materials from which the soil was formed (Lavelle & Spain, 2001), this argument is less probable in the case of the present study, as the sites were adjacent to each other, and had the same underlying soil types (Rebelo *et al*., 2006). Two alternatives explanations might explain differences observed:

Firstly, the herbivores through faeces and urine, transport nutrients from areas where they graze and redistribute them to areas within paddocks where they spend more time (Owen-Smith, 1999; Vallentine, 2001). Through this process, herbivores may create spatial variation in nutrient concentration within the system (Seagle *et al.*, 1992). Additionally, plants take up basic cations (Mg, Na, K, and Ca) to fulfil their physiological requirements (Dahlgren *et al.*, 1997; Lavelle & Spain, 2001). However, herbivores that grazed those plant materials transport those cations to other places, creating a deficit in basic cations (Etherington, 1975), which is not replaced. This thus disrupts the nutrient cycling in the grazed system. Since my plots were not located near water-points, nor resting areas where dung was abundant (personal observation), these areas could be considered as nutrient pools from which herbivores obtain their nutrients. These nutrient pool areas were then simply impoverished in basic cations, thus creating a low pH. In addition, the loss of nutrients through animal harvesting and the exportation of animal products could also be important as hunting has been practiced for over twenty years at the high grazing site. Thus, the affirmation made by Owen-Smith (1999) that the loss of nutrients through animal harvesting is not important in extensive systems is questionable in the present case.

Alternatively, as low soil pH values indicate high mineralization through the presence of organic acid in the soil solution, nutrient decomposition (high accumulation of organic matter

therefore organic acid) could be highest at the high grazing intensity through dung and urine deposition (Mapfumo *et al.*, 2000). The results show that in summer, the nitrate value was high, indicating a high nitrification process. This process is an acid producing reaction (Conyers *et al*., 1995), and may thus explain the low pH value (Haynes & Mokolobate, 2001).

Seasonal variation and grazing by large herbivores affect soil properties (Georgiadis & McNaughton, 1990, Baron *et al.*, 2001, Augustine *et al.*, 2003), with pH and soil moisture content positively following the rainfall regime of the area (Rebelo *et al*., 2006). Except for the seasonal increase in rainfall in the area, no other explanations can be made on the factors affecting soil moisture variation. During winter, temperature in the lowland fynbos and renosterveld eco-region is low, whereas the rainfall reaches its peak (Rebelo *et al.*, 2006). The increase of ammonium and nitrate levels in winter could result in a decrease of soil pH because of a production of organic acids during decomposition (Conyers *et al*., 1995). However, this increase is not efficient in affecting the pH value significantly, and moisture might play a greater role in the rise of soil pH. Therefore, there does not seem to be a simple relationship between soil pH, soil nutrients and microbial activities in the system, as the rise of nutrient concentration does not necessarily affect pH as expected.

### 4.4.2 Soil nutrients

In undisturbed soil, where there were no anthropogenic manipulations, values of carbon to nitrogen ratios are relatively constant and their shifts are very slow (Lavelle & Spain, 2001). The ratio of carbon to nitrogen decreases after two or three decades of herbivore manure deposition (Sommerfeldt *et al.*, 1988). Results obtained in this study appeared to demonstrate that the period of grazing had a greater effect on the ratio of carbon to nitrogen compared to the stocking rate.

The transformation of organic nitrogen to ammonium and nitrate is one of the most important steps of mineralization. Mineralisation processes depend on temperature, soil moisture, aeration, type of organic matter, pH but also on soil type (Dahnke & Vasey, 1973; Jenkinson, 1981). In summer, the concentration of ammonium was lower compared to winter at the medium grazing pressure, but no significant differences were observed between summer and winter. Results for soil ammonium concentration of this study were in part contradictory to the findings of McNaughton *et al.* (1997) that the production of ammonium was positively correlated with grazing intensity. However, the variation of ammonium concentrations

recorded were similar to the findings of Shariff *et al.* (1994), nitrogen levels under medium grazing were lowest via decomposition of organic matter as compared to the high grazing and control site. Therefore, it appears that under medium grazing intensity, nitrogen release is reduced.

The levels of nitrate at the high and medium grazing intensities did not differ between summer and winter, in contrast to nitrate levels at the low grazing intensity. In summer, nitrate levels were lower at the low grazing site than at the other two sites. This indicates that nitrification is high at both the high and the medium grazing intensities. Therefore, it seems that grazing either increases nitrification or maintains nitrate at a relatively constant concentration. Grazing, therefore, maintains high mineral nitrogen in the soil (Seagle *et al*., 1992), especially in summer for this study. Previous studies reported that animals provide mineral nitrogen to the soil through dung and urine deposition (Ruess & McNaughton, 1987; Seagle *et al.*, 1992; Jaramillo & Detling, 1992; McNaughton *et al.*, 1997; Frank & Groffman, 1998; Augustine *et al.*, 2003).

However, at the low grazing intensity, nitrate uptake by plants, micro-organisms (low activity under a water deficit) and nitrogen lost through gases in summer are not compensated for (Lavelle & Spain, 2001). This might have lead to the low levels of nitrate at the low grazing intensity in summer. The high nitrate concentration at the low grazing intensity in winter was most likely due to an increase in microbial activities, thus leading to an increased production of nitrate (Williams & Gray, 1974). This nitrate in excess is not taken up by plants since there are no demands to replace tissue likely due to the lack of herbivory. Thus, it remains high compared to the sites experiencing medium and high grazing intensities where herbivores, through grazing, use it. As a result, the concentration of the soil nitrate remains constant under the present grazing pressure.

Phosphorus is entering the soil largely through organic matter decomposition (Lavelle & Spain, 2001), e.g. of animal dung or animal carcasses, especially under heavy grazing pressure (Etherington, 1975). For instance, in a pastoral system, it has been reported that grazing affects the amount of phosphorus present in the soil (Katznelson, 1997). In winter, as the fresh dung is washed into the soil by water, the readily available phosphorus in the soil increases (Katznelson, 1997). The expected increase of phosphorous in winter could only be observed for the high grazing site.

In summer, soil moisture was low, which means that the ability of plants to absorb phosphorus might be reduced due to immobilization by micro-organisms (Lavelle & Spain, 2001). This implies that the production of phosphorus at both the low and medium grazing sites was not sufficient to supply the below ground demand. However, in winter, moisture was high, therefore the high value might have increased the phosphorus uptake by plant and micro-organisms (i.e. soil phosphorus decreased). Conversely, at the high grazing intensity the "over supply" of phosphorus through herbivore dung and urine might sustain the high soil phosphorus resulting in a decrease of the immobilization process (Cole *et al.*, 1977).

Through the increase in the soil moisture, mineralisation by micro-organism activities increases. Previous investigation has shown that mineralisation of soil organic matter increased gradually as soil water content increased (Black, 1968). Additionally, the low ammonium concentration in summer could occur as a result of the high loss of gaseous nitrogen (Lavelle & Spain, 2001; Xu *et al.*, 2008). However, in winter, the pH value and soil moisture increased, which could also lead to an increase in the activity of soil micro-organisms, regardless of the temperature. Temperature is excluded as potentially having a major effect on soil micro-organisms' activities since the majority of soil micro-organism are mesophile (Optimum growth 25-37 ºC), with an effective minimum temperature of between 5-10 ºC (Dickinson, 1974). In the Western Cape region of South Africa, especially in Swartland Alluvium Fynbos, the average temperature ranges between 6.0 ºC and 29.5 ºC - throughout the year (Rebelo *et al.*, 2006), and was likely not effective in stopping mineralization in the area. Instead, moisture could be the major driver of the mineralisation process.

**4.5 Conclusion**

The results in this study showed that in lowland fynbos and renosterveld, grazing intensity affected soil properties studied. Under a high grazing intensity, soil pH is maintained at relatively low levels, regardless of seasonal change. Under low and medium grazing intensity, pH values and moisture showed the same trend. In addition, under a high stocking rate, the effect of herbivores through trampling on soil moisture levels (Holechek *et al*., 1999; Walters & Martin, 2003) are most noticeable in autumn. The findings of this study agree with previous studies that large herbivores distribute nutrients within the system and have particularly important effects on soil properties as they are organizers of nutrient cycling (McNaughton *et al*, 1988; Danckwerts, 1989; Owen-Smith, 1999). Ammonium concentration

was lowest under a moderate grazing intensity in both winter and summer, whereas nitrate fluctuated significantly from summer to winter in the absence of herbivores. Therefore, herbivores regulated ammonium and nitrate in the soil and, at a high stocking rate, increased the phosphorus concentration to the soil, which probably might supply enough phosphorus to the micro-organisms as well as satisfying plant demand. There were no obvious linear relationships observed between ammonium, nitrate and pH. Therefore, it seems that other processes not taken into account this study could have influenced each one of them. The levels of soil nutrients, pH and moisture are not related. Stocking rates for game in the area investigated need to be carefully considered to avoid negative effects on soil properties.

**4.6 References**


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# Chapter 5: Discussion and Conclusion

## 5.1 General discussion

The ultimate aim of this study was to provide guidelines for appropriate grazing management of the remaining natural fynbos and renosterveld patches. To achieve this goal, the study investigated and compared variations of forage preference of large herbivores, their effect on plant chemical compounds and on soil properties across a grazing intensity over four seasons in a Swartland Alluvium Fynbos / Swartland Shale Renosterveld mosaic. In general, this project was designed to inform farmers and landowners who wish to stock indigenous game in the remaining natural habitats.

Many studies have recognized the importance of herbivores in maintaining plant diversity (Hartnett *et al.*, 1996), ecosystem stability (McNaughton *et al.*, 1988), seed dispersal (Shiponeni & Milton, 2006), and their input into soil properties (Proffitt *et al.*, 1993; Ruess & McNaughton, 1988; Liebig *et al.*, 2006). However, in South Africa, especially in the South-West, little information is available in this field. In fynbos and renosterveld vegetation types, the impact of large herbivores on plant chemical responses and on soil properties is poorly understood. The lack of historical records has created a gap in our knowledge, limiting our ability to build a conceptual framework to guide grazing management in the remaining fragments.

The study was carried out in a Swartland Alluvium Fynbos / Swartland Shale Renosterveld mosaic near Wellington (Rebelo *et al.*, 2006). This is a part of the winter rainfall region of the Cape Floristic Region (CFR) of South Africa. The vegetation types are regarded as critically endangered because more than 75 % has already been transformed in favour of agricultural production and urban settlement (Krug, 2004; Rebelo *et al.*, 2006).

Examinations made at Elandsberg Private Nature Reserve and Krantzkop ammunition factory suggest that grazers, such as eland and bontebok, tend to move alien seed from old fields to natural vegetation. This finding matches with the result of Shiponeni and Milton (2006) who attributed seed dispersal in Renosterveld to the distribution of large mammalian herbivores. These grazers are dispersal agents of alien grasses, potentially moving the seeds of alien grasses into natural vegetation. In addition, seeds of indigenous grasses represented less than

50 % of the seedlings that emerged from dung samples. These findings suggest that herbivory in this system might in fact constrain restoration efforts.

The result of the present study, in line with findings of Barroso (2003), showed that grazing affects plant palatability through its effect on chemical compounds of the grazed plant. Compounds such as tannin and carbohydrate concentration vary under different grazing intensities (e.g. Van Hoven, 2002). The prediction was that plant compounds would differ between low, medium and high grazing intensities and that compounds such as tannin, crude fibre and carbohydrate would be higher at the high grazing intensity and lower under low grazing. My findings demonstrated that plant chemical concentration differed between grazing intensity; however, these differences under different grazing pressure are species and plant age related (Hester *et al.*, 2006). The observations of species response to grazing led to the following categories of plant species recorded: (1) Species that are grazing tolerant and produce more carbohydrates when grazed, and (2) species that are grazing intolerant and produce chemical compounds to deter herbivore damages (Danckwerts & Teague, 1989; Ras, 1990; Danckwerts, 1993; Wolfson, 1999; Agrawal, 2000). The decline in carbohydrate content of some species under heavy grazing can be explained by target species starving its carbohydrate reserves to replace tissue lost from herbivory (Wolfson, 1999). No evidence could be found to suggest that high plant palatability is related to high crude protein, low fibre and low tannin concentrations as predicted. Therefore, the results support in part the conclusion of Katjiua (2006) that forage preference cannot be related to absolute levels of nutrients and antifeedant compounds, but rather on the ratio of those nutrients and antifeedant compounds. Chemical or physical properties not taken into account in this study could play a role in determining palatability and preference. For instance, specific minerals such as calcium and potassium, specific fibres such as cellulose and hemicellulose, or even soil physical and chemical properties could have had an impact on the results observed (Black, 1957; Georgiadis & McNaughton, 1990). Nevertheless, this study contributes to the understanding of the complexity of plant-animal interactions in a fynbos-renosterveld mosaic. Additionally, it provides an indication that a combination of chemical compounds and specific stage of plant growth at a specific season of the year shapes plant palatability and herbivore preference. The magnitude of each plant chemical compound's response varies from one species to another and from one season to another under the different grazing intensities.

The comparison of soil properties investigated in this study showed that grazing intensities affect soil nutrient levels, pH and soil moisture to some extent. Heavy grazing intensity maintains pH values at relatively low-levels regardless of seasonal change, whereas under low and medium grazing intensity, pH increases with an increase in moisture. These findings are, however based on correlations, which do not necessarily imply causation. In addition, the observations recorded in autumn led to the conclusion that the effect of high grazing pressure on soil moisture is more obvious under moist conditions (see also Walters & Martin, 2003), and offer surplus phosphorus to the soil, which in turn could fulfil the needs of soil micro-organisms as well as the plants. Herbivores seem to regulate the soil ammonium and nitrate concentration by keeping it at relatively constant levels in the soil. My findings confirm those reported by McNaughton *et al.* (1988) and Owen-Smith (1999) that large herbivores have important effects on soil properties by improving the soil nutrient flow, soil nutrient cycling and principally nutrient distribution. Contrary to my hypothesis, the results also indicated that the concentration of available nitrogen in the soil was not the highest at the high grazing intensity in all seasons. Soil ammonium and nitrate concentrations show patterns which were not linear. From this, the conclusion may be drawn that in the fynbos-renosterveld mosaic investigated, each of the soil parameters measured could have been influenced by other biological processes not taken into account in this study (Hayes, 1991).

**5.2 Plant chemical compounds, soil properties and herbivore interactions**

Soil pH governs the activities of micro-organisms and the decomposition rate of soil organic matter (Sumner *et al.*, 1991). Throughout the year, the soil pH value recorded at the high grazing intensity was the lowest, thus, the high grazing intensity could affect the metabolic activity of some plant species unable to grow at a low pH (i.e. Acidophobe plant species).

In summer, the protein content of *Montinia caryophyllaceae* is about double at the low grazing intensity compared to the high grazing intensity. Working on the assumption that *M. caryophyllaceae* uses nitrate as a source of nitrogen, the foregoing protein concentration (indicator of the nitrogen content of the plant) is inversely related to the concentration of soil nitrate in summer between both the low and the high grazing intensity. This observation implies that the concentration of nitrogen in the soil could not necessarily reflect the representation of protein in the plant. Other mechanisms such as grazing through the removal of leaves could lead to a change in plant nutrient concentration even though the soil properties are not the limiting factor. In contrast to *M. caryophyllaceae*, species such as *Tribolium*

*unioleae* show no significant differences with regard to the grazing intensity or to the soil nitrate concentration. This species might take up ammonium as a source of nitrogen. However, if it takes up nitrate as nitrogen source, it means that *T. unioleae* is not affected by the grazing intensity or the concentration of nitrate in the soil in summer. Therefore, the way a species responds to grazing is species specific. In addition, the soil properties have less influence on plant chemical response than grazing, in the fynbos-renosterveld mosaic.

### 5.3 Recommendations for future research

Further studies in this field would need to consider the parameters that were not included in the current study but may however play an important role in shaping the patterns observed. For example, a study on the establishment of alien species around water points, resting areas and herbivores tracks in natural vegetation will shed a light onto the dispersal of alien species by large herbivores. This will provide the possibility to determine potential further alien invasion into the remaining natural vegetation. Another aspect could be the investigation of soil nutrient levels in resting areas, around water points and in grazed areas, determining source-sink dynamics of soil nutrients and basic cations, which could explain the low pH in the highly grazed sites such as Krantzkop. A further focus can be placed on the study of microbial activities in relation to the seasonal variation under different grazing intensities. The effects of grazing on specific minerals such as magnesium, iron and copper, which may explain the rate of herbivore birth or mortality in the area, also warrants further investigation.

### 5.4 Management recommendations

The knowledge on plant-herbivore interactions in fynbos and renosterveld is still limited. To determine the appropriate grazing management, knowledge on the capacity of the remaining natural fragment to sustain wild herbivores is required (Bothma, 2002). Thus, manager should have good knowledge of the diet of all animals on its game ranch, as a proper diet is indispensable for game survival (Bothma, 2002). This study indicates that a moderate grazing intensity 0.09 LAU/ha is the best management for fynbos and renosterveld veld types, as this result in less tanniferous compounds production in food plants. It also shows that stocking rates for game in the area needs to be carefully considered to avoid negative effects on soil properties. Therefore, information provided by scientific studies contributes to a positive relationship between game stocking rates, soil properties and vegetation quality. Based on the

results of the study, I can make the following recommendations for the management of the area:

Firstly, improve the re-establishment opportunities for natural veld in order to decrease the spread of alien species dispersed by indigenous game. Secondly, before any game is introduced in an area, a study determining the ecological ability of the natural vegetation to sustain game species is required (Bothma, 2002). My study suggests that animals should be kept at moderate stocking rates of 0.09 LAU / ha since the production of tannin is reduced and thus could have a lesser impact on ranch conditions and probably on animal production (Tainton *et al.*, 1999). However, native tanniferous species such as *Ficinia sp.*, *Montinia caryophyllaceae* and *Ischyrolepis capensis* should not be removed, because they could be of importance in the system. Tannin has an antiparasitic activity that can have beneficial effects on herbivore health (Haring *et al.*, 2007). Lastly, the spread of indigenous grass which can meet the basic needs for growth and other physiological functions of grazers should be promoted, and their nutritional status investigated in order to know whether they meet the nutritional requirements of grazers in the system.

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Appendix A. List of species, and their families, selected for chemical analysis

| Family | Scientific name |
|---|---|
| Asteraceae | *Elytropappus rhinocerotis* |
| Cyperaceae | *Ficinia indica* |
| Cyperaceae | *Ficinia sp.* |
| Montiniaceae | *Montinia caryophyllacea* |
| Poaceae | *Briza maxima* |
| Poaceae | *Cynodon dactylon* |
| Poaceae | *Ehrharta sp.* |
| Poaceae | *Eragrostis sp.* |
| Poaceae | *Grass 3* |
| Poaceae | *Grass 4* |
| Poaceae | *Hyparrhenia hirta* |
| Poaceae | *Lolium sp.* |
| Poaceae | *Schismus barbata* |
| Poaceae | *Themeda triandra* |
| Poaceae | *Tribolium unioleae* |
| Poaceae | *Vulpia myoros* |
| Restionaceae | *Eligia stipularis* |
| Restionaceae | *Ischyrolepis capensis* |
| Restionaceae | *Ischyrolepis sp2* |
| Restionaceae | *Ischyrolepis sp3* |

Appendix B. List of species recorded in natural vegetation at Voëlvlei, Elandsberg and Krantzkop throughout the year of sampling. * indicates alien species

| Family | Scientific name | comment |
|---|---|---|
| Aizoceae | *Aizoon sp.* | |
| Aizoceae | *Erepsia patula* (Haw.) Schwantes. | |
| Aizoceae | *Galenia africana L.* | |
| Aizoceae | *Lampranthus cf. elegans* (Jacq.) Schwantes | |
| Aizoceae | *Lampranthus sp.* | |
| Anacardiaceae | *Rhus angustifolia* L. | |
| Apiaceae | *Centella capensis* L. | |
| Apiaceae | *Lichtenstenia sp.* | |
| Apocynaceae | *Asclepias crispa* J.B. Bergius. | |
| Asparagaceae | *Asparagus rubicundus* P.J. Bergius. | |
| Asparagaceae | *Asparagus sp.* | |
| Asphodelaceae | *Trachyandra sp.* | |
| Asteraceae | *Anthanasia sp.* | |
| Asteraceae | *Arctotis acaulis* L. | |
| Asteraceae | *Arctotis arhistia.* | |
| Asteraceae | *Arctotis sp.* | |
| Asteraceae | *Athanasia crenata* L. | |
| Asteraceae | *Berkheya armata* (Vahl) Druce | |
| Asteraceae | *Corymbium africanum* L. | |
| Asteraceae | *Elytropappus rhinocerotis* (L.f.) Less. | |
| Asteraceae | *Eriocephalus africanus* L. | |
| Asteraceae | *Felicia bergerana* (Spreng.) O.Hoffm. | |
| Asteraceae | *Felicia sp.* | |
| Asteraceae | *Gazania sp.* | |
| Asteraceae | *Gnaphalium sp.* | |
| Asteraceae | *Helichrysum asperum* (Thunb.) Hilliard & B.L.Burtt. | |
| Asteraceae | *Helichrysum cylindriflorum* (L.) Hilliard & B.L.Burtt. | |
| Asteraceae | *Helichrysum sp.* | |
| Asteraceae | *Helichrysum territifolium* (L.) D.Don | |
| Asteraceae | *Leysera gnaphaloides* (L.) L. | |
| Asteraceae | *Metalasia fastigiata* (Thunb.) D.Don | |
| Asteraceae | *Metalasia sp.* | |
| Asteraceae | *Relhania fruticosa* (L.) K.Bremer | |
| Asteraceae | *Senecio pubigerus* L. | |
| Asteraceae | *Senecio sp.* | |
| Asteraceae | *Stoebe sp.* | |
| Asteraceae | *Tripteris tomentosa* (L.f.) B.Nord. | |
| Asteraceae | *Ursinia anthemoides* (L.) Poir. | |
| Asteraceae | *Ursinia sp.* | |
| Boraginaceae | *Echiostachys incanus* (Thunb.) Levyns. | |
| Boraginaceae | *Lobostermom sp.* | |
| Campanulaceae | *Lobelia sp.* | |
| Campanulaceae | *Prismatocarpus fruticosus* L'Hér. | |
| Campanulaceae | *Roella ciliata* L. | |
| Campanulaceae | *Wahlenbergia capensis* (L.) A.DC. | |
| Caryophyllaceae | *Silene gallica* L.* | *alien* |
| Caryophyllaceae | *Stellaria sp.* | |
| Colchicaceae | *Baeometra uniflora* (Jacq.) G.J.Lewis | |
| Compositae | *Gymnodiscus capillaris* (L.f.) DC. | |

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|---|---|---|
| Crassulaceae | *Crassula ciliata* L. | |
| Crassulaceae | *Crassula flava* L. | |
| Cyperaceae | *Ficinia indica* (Lam.) Pfeiff. | |
| Cyperaceae | *Ficinia oligantha* (Steud.) J.Raynal | |
| Cyperaceae | *Ficinia sp.* | |
| Cyperaceae | *Tetraria sp.* | |
| Dipsacaceae | *Scabiosa incisa* Mill. | |
| Ebenaceae | *Euclea acutifolia* E.Mey. ex A.DC. | |
| Ericaceae | *Erica coarctata* J.C.Wendl. | |
| Ericaceae | *Erica sp.* | |
| Euphorbiaceae | *Euphorbia arceuthobioides* Boiss | |
| Fabaceae | *Aspalathus aculeata* Thunb. | |
| Fabaceae | *Aspalathus acuminata* Lam. | |
| Fabaceae | *Aspalathus attenuata* R.Dahlgren. | |
| Fabaceae | *Aspalathus cf. horizontalis* R. Dahlgren. | |
| Fabaceae | *Aspalathus ciliaris* L. | |
| Fabaceae | *Aspalathus cordata* R. Dahlgren. | |
| Fabaceae | *Aspalathus ericifolia* L. | |
| Fabaceae | *Aspalathus perforata* (Thunb.) R.Dahlgren. | |
| Fabaceae | *Aspalathus sp.* | |
| Fabaceae | *Aspalathus spinosa L.* | |
| Fabaceae | *Aspatathus sp.* | |
| Fabaceae | *Indigofera sp.* | |
| Fabaceae | *Podalyria cf. biflora* (L.) Lam. | |
| Fabaceae | *Trifolium angustifolium* L.* | *alien* |
| Fabaceae | *Trifolium sp.** | *alien* |
| Gentianaceae | *Chironia linoides* L. | |
| Geraniaceae | *Pelargonium lobatum* (Burm.f.) L'HTr. | |
| Geraniaceae | *Pelargonium longifolium* (Burm.f.) Jacq. | |
| Geraniaceae | *Pelargonium myrrhifolium* (L.) L'HTr. | |
| Geraniaceae | *Pelargonium sp.* | |
| Hyacinthaceae | *Albuca juncifolia* Baker. | |
| Hyacinthaceae | *Albuca sp.* | |
| Hyacinthaceae | *Lachenalia sp.* | |
| Hyacinthaceae | *Lachenalia unifolia* Jacq. | |
| Iridaceae | *Aristea africana* L.Hoffmanns. | |
| Iridaceae | *Babiana odorata* L.Bolus. | |
| Iridaceae | *Babiana secunda* (Thunb.) Ker Gawl. | |
| Iridaceae | *Babiana sp.* | |
| Iridaceae | *Geissorhiza sp.* | |
| Iridaceae | *Hexaglottis lewisiae* Goldblatt subsp. secunda Goldblatt | |
| Iridaceae | *Lapeirousia azurea* (Eckl. ex Baker) Goldblatt | |
| Iridaceae | *Micranthus alopecuroides* (L.) Rothm. | |
| Iridaceae | *Micranthus tubulosus* (Burm.) N.E.Br. | |
| Iridaceae | *Moraea cf. lewisiae* (Goldblatt) Goldblatt | |
| Iridaceae | *Moraea viscaria* (L.f.) Ker Gawl. | |
| Iridaceae | *Ornithogalum conicum* Jacq. Jacq. | |
| Iridaceae | *Ornithogalum thyrsoides* Jacq. | |
| Iridaceae | *Romulea sp.* | |
| Iridaceae | *Thereianthus sp.* | |
| Iridaceae | *Thereianthus spicatus* (L.) G.J.Lewis var. spicatus | |
| Lamiaceae | *Salvia africana-caerulea* L. | |
| Lauraceae | *Cassytha ciliolata* Nees | |
| Lobeliaceae | *Cyphia phyteuma* (L.) Willd. | |

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|---|---|---|
| Malvaceae | *Hermannia althaeifolia* L. | |
| Malvaceae | *Hermannia scabra* Cav. | |
| Malvaceae | *Hermannia sp.* | |
| Molluginaceae | *Polpoda stipulacea* (Leight.) Adamson | |
| Montiniaceae | *Montinia caryophyllacea* Thunb. | |
| Oxalidaceae | *Oxalis commutata* Sond. | |
| Oxalidaceae | *Oxalis obusta* Jacq. | |
| Oxalidaceae | *Oxalis pes-caprae* L. var. sericea (L.f.) Salter | |
| Oxalidaceae | *Oxalis sp.* | |
| Poaceae | *Aristida diffusa* Trin. | |
| Poaceae | *Aristida junciformis* Trin. & Rupr. | |
| Poaceae | *Avena barbata* Pott ex Link.* | *alien* |
| Poaceae | *Briza maxima* L.* | *alien* |
| Poaceae | *Briza minor* L.* | *alien* |
| Poaceae | *Bromus diandrus* Roth.* | *alien* |
| Poaceae | *Bromus pectinatus* Thunb.* | *alien* |
| Poaceae | *Cymbopon marginatus* (Steud.) Stapf ex Burtt Davy | |
| Poaceae | *Cynodon dactylon( L.) Pers.* | |
| Poaceae | *Ehrharta calycina* Sm. | |
| Poaceae | *Ehrharta melicoides* Thunb. | |
| Poaceae | *Ehrharta sp.* | |
| Poaceae | *Ehrharta vilosa* Schult.f. | |
| Poaceae | *Eragrostis capensis* Thunb. | |
| Poaceae | *Eragrostis curvula* (Schrad.) Nees | |
| Poaceae | *Eragrostis sp.* | |
| Poaceae | *Festuca scabra* Vahl | |
| Poaceae | *Hyparrhenia hirta* (L.) Stapf | |
| Poaceae | *Lepidium sp.* | |
| Poaceae | *Lolium sp.** | *alien* |
| Poaceae | *Melinis repens* (Willd.) Zizka | |
| Poaceae | *Pentaschistis airoides* (Nees) Stapf (Nees) Stapf | |
| Poaceae | *Pentaschistis barbata* (Nees) H.P.Linder (Nees) H.P.Linder. | |
| Poaceae | *Pentaschistis curvifolia* (Schrad.) Stapf | |
| Poaceae | *Pentaschistis pallida* (Thunb.) H.P.Linder. | |
| Poaceae | *Plantago sp.* | |
| Poaceae | *Poa annua L.** | *alien* |
| Poaceae | *Schismus barbatus* (Loefl. ex L.) Thell. | |
| Poaceae | *Stipagrostis sp.* | |
| Poaceae | *Stipagrotis zeyheri* (Nees) De Winter ssp. zeyheri | |
| Poaceae | *Themeda triandra* Forssk. | |
| Poaceae | *Tribolium hispidum* (Thunb.) Desv. | |
| Poaceae | *Tribolium unioleae* (L.f.) Renvoize | |
| Poaceae | *Vulpia myuros* (L.) C.C.Gmel.* | *alien* |
| Polygalaceae | *Muraltia ericaefolia* DC. | |
| Polygalaceae | *Muraltia filiformis* (Thunb.) DC. var. filiformis. | |
| Polygalaceae | *Muraltia sp.* | |
| Polygalaceae | *Polygala scabra* L. | |
| Polygalaceae | *Polygala umbellata* L. | |
| Polygonaceae | *Rumex cordatus* Poir.* | *alien* |
| Proteaceae | *Leucadendron corymbosum* P.J.Bergius | |
| Proteaceae | *Leucadendron lanigerum* H.Buek ex Meisn. var. lanigerum | |
| Proteaceae | *Protea mucronifolia* Salisb. | |
| Proteaceae | *Serruria acrocarpa* R.Br. | |
| Proteaceae | *Serruria candicans* R.Br. | |

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|---|---|
| Restionaceae | *Chondropetalum ebracteatum* (Kunth) Pillans. |
| Restionaceae | *Elegia persistens* Thunb. |
| Restionaceae | *Elegia sp.* |
| Restionaceae | *Elegia stipularis* Mast. |
| Restionaceae | *Ischyrolepis capensis* (L.) H.P.Linder |
| Restionaceae | *Ischyrolepis sp.* |
| Rhamnaceae | *Phylica cf. cephalantha* Sond. |
| Rhamnaceae | *Phylica plumosa sp.* |
| Rhamnaceae | *Phylica sp.* |
| Rhamnaceae | *Phylica strigulosa* Sond. |
| Rosaceae | *Cliffortia cf. strobilifera* L. var. longifolia Eckl.&Zeyh. |
| Rosaceae | *Cliffortia juniperina* L.f. |
| Rosaceae | *Cliffortia sp.* |
| Rubiaceae | *Anthospermum aethiopicum L.* |
| Rubiaceae | *Anthospermum galioides* Rchb.f. |
| Rubiaceae | *Anthospermum sp.* |
| Rutaceae | *Agathosma serpyllacea* Licht. ex Roem. & Schult. |
| Rutaceae | *Diosma sp.* |
| Santalaceae | *Thesium funale* L. |
| Santalaceae | *Thesium sp.* |
| Scrophulariaceae | *Chenopodiopsis cf. hirta* (L.f.) Hilliard |
| Scrophulariaceae | *Selago fruticulosa* L. |
| Scrophulariaceae | *Selago sp.* |
| Tecophilaeaceae | *Cyanella hyacinthoides* L. |
| Thymelaeaceae | *Gnidia sp.* |
| Zygophyllaceae | *Zygophyllum sp.* |